# Investigations on tree species suitable for the recultivation of degraded land areas in Central Amazonia

**(SHIFT project BMBF 0339638A and 01LT0005 / CNPq ENV 42-2)**

From May 1, 1998 to April 30, 2001

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Institute of Wood Biology, Hamburg University, Hamburg: Prof. Dr. J. Bauch, Dr. O. Dünisch
Centro de Pesquisa Agroflorestal da Amazonia Ocidental/Empresa Brasileira da Pesquisa Agropecuária (EMBRAPA, Amazonia Ocidental), Manaus: Dr. L. Gasparotto, C. de Azevedo, R. de Lima, R. de Morais

Cooperation: University of Paraná, Curitiba: Prof. Dr. Reissmann, Dr.E. Neves



# Annual Report 2000

(From January 1, 2000 to December 31, 2000)

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## Abstract

**Investigations on tree species suitable for the recultivation of degraded land areas in Central Amazonia**

In Central Amazonia, an increasing demand for high quality wood and wood products is obvious for the local market and for the export. Therefore it is recommended to consider for the recultivation of degraded land areas in polyculture systems also trees for wood production. However, only few knowledge is available how to manage a sustainable growth of the selected species *Swietenia macrophylla* King, *Carapa guianensis* Aubl., *Cedrela odorata* L., *Dipteryx odorata* (Aubl.) Willd., and *Hymenaea courbaril* L. under the conditions on the „terra firme" in Central Amazonia.

In cooperation with the EMBRAPA, Amazonia Ocidental in Manaus and three German projects (ENV 23, ENV 45, ENV 52), in the year 2000 we especially investigated (1) photosythesis and carbohydrate allocation and (2) the plant-water relationships of the selected tree species. Special emphasis was given to the 3 species of the family *Meliaceae*. Comparative experiments have been done for monocultures, polycultures, enrichment cultures, and primary forests.

(1) The seasonal variation of the net photosynthesis, the content of soluble carbohydrates, starch, and protein as well as the biomass production of 7-year-old *Swietenia macrophylla* King, *Carapa guianensis* Aubl. and *Cedrela odorata* L. were investigated in a plantation near Manaus, Central Amazon. The study responds to the demand for the recultivation of highly exploited native tree species of the Amazon with plantations considering also high quality wood production. Gas exchange measurements showed that the mean annual net photosynthesis of *Carapa* was significantly higher (0.78 µmol $CO_2$ $m^{-2}$ $s^{-1}$) compared to the mean annual net photosynthesis of *Swietenia* (0.10 µmol $CO_2$ $m^{-2}$ $s^{-1}$) and *Cedrela* (0.28 µmol $CO_2$ $m^{-2}$ $s^{-1}$). The net photosynthesis and the content of reserve carbohydrates found in *Swietenia* and *Cedrela* followed an annual pattern showing a decrease of the net photosynthesis and an increase of reserve carbohydrates in the biomass (13-19 % and 10-16 % of oven dry biomass, respectively) during the drier period from June until November. A seasonal variation of the protein content of *Swietenia* indicated that in periods with a reduced carbohydrate supply protein serves also as a food reserve in this species. In contrast no annual course of the net photosynthesis and the content of reserve material was found in *Carapa*. Corresponding to the $CO_2$ gas exchange measurements the annual relative growth rate of *Swietenia* (4 %) and *Cedrela* (9%) was lower than the relative growth rate of *Carapa* (14 %), although respiration of *Swietenia* and *Cedrela* were only 49 % and 45 % of the annual net photosynthesis compared to 58 % calculated for *Carapa*. From these findings it was concluded that the site conditions in the plantation are not optimal for sustainable growth of *Swietenia* and *Cedrela*, whereas *Carapa* is better adapted to the alteration of site conditions in plantations compared to the natural habitat of the species. This is mainly due to the higher photosynthetic capacity of this species and a major indirect allocation of leaf assimilates via short-term storage and mobilisation of reserve carbohydrates. This pathway for assimilate allocation is highly energy consuming, but offers better conditions for the adaptation to intra-annual changes of exogenous input compared to a direct

assimilate allocation from net photosynthesis to the meristems as predominantly found in *Swietenia* and *Cedrela*.

(2) The regulation of xylem sap flow by stomata opening, osmotic pressure, and the use of stored xylem water in an evergreen (*Carapa guianensis* Aubl.), in a semi-deciduous (*Swietenia macrophylla* King), and in a deciduous (*Cedrela odorata* L.) *Meliaceae* species was studied in a 7-year-old plantation near Manaus, Brasil. The investigations respond to the increasing demand for knowledge on plant-water relationships of highly exploited timber trees of the Amazon. Xylem sap flow measurements by means of constant heat flow method showed, that the total daily sap flow of *Carapa* (3.8 l $day^{-1}$ to 16.4 l $day^{1}$) exceeded the total daily sap flow of *Swietenia* (2.4 l $day^{1}$ to 7.0 l $day^{1}$) and *Cedrela* (1.6 l $day^{1}$ to 11.6 l $day^{1}$) during the whole year, whereas maximum sap flow velocity was measured in *Cedrela* (7.03 m $h^{-1}$, *Carapa*: 3.69 m $h^{-1}$, *Swietenia*: 1.67 m $h^{-1}$). A decrease of xylem sap flow correlated with a decrease of the soil water potential and an increase of the vapour saturation deficit of the air, was more pronounced in the deciduous (*Cedrela*) and semi-deciduous species (*Swietenia*) compared to the evergreen species (*Carapa*). The higher total daily sap flow of *Carapa* compared to *Swietenia* and *Cedrela* was correlated with the higher leaf biomass and the higher sapwood portion of this species, whereas the high sap flow velocity in the outer xylem of *Cedrela* was correlated with the larger vessel size of this species. The seasonal variation of xylem sap flow of the 3 species was correlated with the opening and closure of the leaf stomata studied by infiltration experiments, but intra- and inter-diurnal variation of stomata opening and closure was more pronounced in *Swietenia* compared to *Carapa* and *Cedrela*. High cell osmotic pressure of paratracheal parenchyma cells (up to 1100 mosmol $l^{-1}$) due to a high content of K and soluble sugars contributed to the xylem sap flow of *Carapa* during the driest period of the year, whereas maximum osmotic potentials of paratracheal parenchyma cells of *Swietenia* and *Cedrela* were found during drier periods of the wet season and during the wettest months, respectively. Stem water storage contributed in *Carapa* with 14 % to 35 % and in *Swietenia* with 13 % to 25 % to the daily water balance , whereas xylem water storage was negligible for the daily water balance of *Cedrela*. From these findings it was concluded that the evergreen species *Carapa guianensis* compensates best a reduced water supply, whereas water uptake of the semi-deciduous and the deciduous species *Swietenia macrophylla* and *Cedrela odorata* depends on a high soil water content, which can be used more efficiently by *Cedrela* than by *Swietenia*.

In cooperation with the SHIFT projects ENV 23 (AG Prof. Dr. Lieberei) and 45 (AG Prof. Dr. Zech) the study on plant-water relationships were extended to *Bertholettia excelsa*. In addition a study for a PhD. thesis of Ronaldo R. Morais was started, who got a 3-year-grant from the CNPq Brasilia within our project ENV 42-2 (01LT0005/3)

# Content

## 1. Introduction and approach of the second phase of the project

Due to the strong demand for sustainable wood production in the Amazon, since 1995 investigations on suitable tree species for wood production in plantations on the „terra firme" of the Central Amazon are carried out within the SHIFT project 0339638 A/ENV 42. The study is concentrated at the experimental site of EMBRAPA Amazonia Ocidental, located 29 km out of the city of Manaus.

In this study the site conditions (nutrient supply of the soil, water supply of the trees, light) of a traditional monoculture plantation are compared with the site conditions of mixed plantations. The study is carried out from the period of site preparation until an age of 8 years.

As to determine the site demands of eight important native tree species of the Amazon (*Swietenia macrophylla, Carapa guianensis, Cedrela odorata, Dipteryx odorata, Hymenaea courbaril, Ceiba pentandra, Virola surinamensis, Tabebuia heptaphylla*) the influence of light, the water supply and the nutrient supply of the soil on the growth dynamics of the trees is studied.

The results obtained during the first phase of the project were published in 1999 in 9 individual contributions within the series „Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft", Hamburg, Nr. 193.

As to get stronger correlations between the site conditions and the growth of the plantation grown trees, during the second phase of the project (since May 1998) the investigations were extended to ecophysiological aspacts. Due to the high significance of light and water supply for most of the selected species special regard was given to primary production and the regulation of the water uptake and release of the species.

The concept of the project ENV 42 is part of the interdisciplanary research program SHIFT (Studies on human impact on forests and floodplains in the tropics) at the EMBRAPA Amazonia Ocidental in Manaus. There are links to ENV 23 (AG. Prof. Dr. Lieberei), ENV 45 (AG Prof. Dr. Zech), ENV 52 (Prof. Dr. Beck) and ENV 102 (Prof. Dr. Vlek).

## 2. Investigations carried out in 2000 and scientific results

### 2.1. Overview of the project activities in 2000

*Carbohydrate supply of the trees:* In 1999 and 2000 the seasonal variation of photosynthesis, the reserve carbohydrate content of *Swietenia, Carapa, Cedrela, Dipteryx,* and *Hymenaea*, the content of soluble sugar (glucose, fructose, sucrose, raffinose, stachyose) and starch of the leaves, the phloem of the stem, the xylem of the stem and of the roots was monthly quantified. Sample collection was carried out from 1998 until September 1999. Sample preparation and carbohydrate analyses are carried out in cooperation with the Institute of Wood Chemistry, Federal Research Center for Forestry and Forest Products, Hamburg. From these data a the carbon balance of the species was intraannually calculated.

In addition the relationship between the light intensity and the net photosynthesis of *Cedrela odorata* was studied under growth chamber conditions in cooperation with the Institute of World Forestry of the Federal Research Center for Forestry and Forest Products in Hamburg (Dr. Kriebitzsch). Corresponding measurements were already carried out for *Swietenia macrophylla* King and *Carapa guianensis* Aubl. in 1999.

*Water supply of the trees:* Besides the quantification of water fluxes in the plantations, studies on the relationship between the transpiration, xylem sap flow, the water potential of the soil, the stem and leaf of the trees and the atmosphere are of main interest as to study in how far the investigated tree species are adapted to drier periods. For this purpose in 2000 xylem water flux measurements of *Swietenia macrophylla, Carapa guianensis* and *Cedrela odorata* and meteorological measurements at the leaf-atmosphere interface of the trees were intensified. As to study the water potential of the leaves, pressure bomb measurements were carried during wet and dry periods.

In 2000 Ronaldo Morais extended these studies to *Dipteryx odorata* and *Bertholletia excelsa* (PhD thesis INPA, Manaus, financial support: PhD grant CNPq, Brasilia and BMBF, Bonn, cooperation: EMBRAPA, Manaus, INPA, Manaus, University of Hamburg).

### 2.2. Scientific results

After six years of experiments the investigations on (1) the photosynthesis and assimilate allocation and (2) the regulation of xylem sap flow of *Swietenia macrophylla* King, Carapa guianensis Aubl. and Cedrela odorata L. were terminated.. In 2000 the data evaluation was carried out and the main aspects are summarized below.

## 2.2.1. Photosynthesis and assimilate allocation of three plantation-grown species of the *Meliaceae* in the Central Amazon

### Introduction

Slash and burn land-use systems (Uhl et al. 1981, Uhl 1987) and logging activities lead to a strong reduction of high quality timber species in the Amazon and in many cases to a degradation of the exploited areas (Lamprecht 1986, Brünig 1996). As to counteract this tendency during the recent years in the Central Amazon special attention was given to the cultivation of native tree species for high quality timber production in plantations (Lamprecht 1986, Whitmore 1995, Brünig 1996, Bauch et al. 1999). Due to the anthropogeneous impact site conditions in plantations are different from those in primary forests (Breda et al. 1995, Oren et al. 1995), which might influence the growth of the planted trees significantly, although native species are selected for planting. Comparative studies carried out in primary forests and in timber plantations of the Amazon showed significant alterations of the light conditions as well as the water and nutrient supply in plantations compared to the natural habitat of the planted species (Szott and Palm 1996). Therefore sound information on growth and demands for light, nutrients, and water of the tree species selected from the primary forest for wood production in plantations is necessary as to select the most promissing ones for sustainable timber production (see also Bauch et al. 1999). Until today for most of the native tree species of the Amazon selected from the primary forest little information on growth and site demands is available.

An understanding of the biomass production and tree growth basically depends on knowledge of production, storage and utilisation of assimilates. Beside genetic factors, many exogenous factors such as light (Collet e al. 1993, Ducrey 1994), nutrient (Küppers et al. 1985, Mc Donald et al. 1992, Stockfors and Linder 1997), and water supply (Dreyer et al. 1991) have a strong influence on the primary production and the efficiency of the conversion of solar energy into biomass. A part of the assimilates obtained from photosynthesis is transformed into storage material. In plants starch, soluble carbohydrates, proteins, and lipids (Bryant et al. 1999) are the major food reserves and have to be considered studying the carbon economy of trees. Respiration for maintaining processes in living cells and growth causes a strong reduction of the biomass production of a tree compared to the total assimilate production during photosynthesis. In addition the net photosynthesis, the storage and mobilisation of food reserves, and the respiration show seasonal patterns related to seasonal changes of exogenous input and growth (Hansen and Beck 1994, Niinemets et al. 1999) as well as intrinsic factors (Zhang et al. 1994, Garcia-Plazaola and Becerril 2000) indicating the demand for time series analyses for significant information on the plant carbohydrate metabolism .

Therefore as to understand the relationship between assimilate production and tree growth of plantation grown tropical tree species in this work seasonal patterns of photosynthesis, storage and mobilisation of food reserves (soluble carbohydates, starch, protein), respiration, and biomass production were investigated. This case study was

concentrated on the seasonal course of net photosynthesis, the content of food reserves, and the relationship of assimilate production and assimilate allocation of *Swietenia macrophylla* King, *Carapa guianesis* Aubl., and *Cedrela odorata* L., three highly exploited species in primary forests of the Central Amazon.

## Material and Methods

### *Site and tree selection*

In January 1992 the Federal Research Center EMBRAPA Amazônia Ocidental, located 24 km out of the city of Manaus (3°8' S, 59°52'W) established experimental plots of 20 economically important tree species. For this study 100 trees of each species were planted with a spacing of 3 m x 3 m. In particular species of the family *Meliaceae* were considered. The area is located at approximately 50 m above sea level with an annual precipitation of about 2,500 mm (Min. 110 mm (August) / Max. 295 mm (February) per month), a mean air temperature of 26.4° C, and a mean humidity of the air of 87 %. According to categorisation, the soil is a poor xanthic Ferralsol (FAO, 1990, Schroth et al. 2000).

For the continuous measurement of photosynthesis and assimilate allocation of *Swietenia macrophylla* King, *Carapa guianensis* Aubl., and *Cedrela odorata* L. carried out from January 1999 until December 1999 and to some extent also in 2000 three trees of each species were selected, representing the three mean trees (median) of the planted collective (comp. Dünisch and Schwarz 2001). In December 1998 the mean tree biomass of *Swietenia,* Carapa, and *Cedrela* was 53 kg, 106 kg, and 61 kg, respectively.

### *Determination of biomass, leaf, stem, and root growth of the trees*

As to select the three mean trees of each species for the experiments the breast height diameter, the tree height, the height of the crown, and the density of the crown of all planted trees were studied. From known allometric relationships between these dendrometric parameters and the tree biomass, the biomass of the 7-year-old *Swietenia, Carapa*, and *Cedrela* trees was calculated with an accuracy of 82 %, 91 %, and 87 % respectively (comp. Dünisch and Schwarz 2001). Based on these biomass data the three mean trees of each species were selected for continuous measurements. At the end of the experiment in January 2000 the experimental trees were excavated and the oven dry biomass (105° C) of the whole tree separated into 9 to 17 tree fractions was quantified.

Budbreak and leaf growth of the experimental trees were monitored in 1999 marking all new leaves of the crown and by means of weekly measurements of the leaf size (Dünisch et al. 1999). As to calculate the leaf biomass the relationship between the leaf size (measured with an optical area meter, LI-Cor, USA) and the oven dry biomass (105° C) of 150 leaves per species was quantified. Calculations of the leaf biomass based on this relationship were carried out highly significant with an error less than 3 %. As to quantify

the litterfall of the trees litterfall collectors (3 m x 3 m) were installed below the experimental trees. Litterfall was collected weekly and the oven dry biomass (105° C) was quantified gravimetrically.

The intra-annual growth dynamics in wood formation of the trees were determined by monthly pin-marking. The cambium was wounded with a scalpel and the wound reaction was studied by light microscopy in cross, radial, and tangential directions (Kuroda and Shimaji 1984). The traumatic resin canals initiated by wounding were suitable for dating of cambial cell divisions. Accurate increment measurements of the stem were possible by means of the "pinning-method" for increments greater than 0.3 mm (comp. Bauch and Dünisch 2000).

The root growth of the trees was studied by root windows of 1 m x 1m installed in the four cardinal directions 50 cm, 100 cm, and 150 cm distant from the stem (Leisen and Marschner 1990, Bauer et al. 1991). The roots observed along the root windows were copied to transparencies in weekly intervals and the growth dynamics of the single roots were analysed comparing the root length and the root diameter from one week to another measured by means of a digitizer board (HIPAD PLUS, Houston Instruments, USA). Comparing the results obtained by this method with results obtained by means of weekly soil samples and a subsequent isolation of fine roots by a washing procedure carried out according to Schroth and Kolbe (1994) differences up to 27 % were found indicating methodical difficulties for accurate measurements of root growth in the field.

*Measurement of the leaf gas exchange*

Leaf gas exchange ($CO_2$ and $H_2O$) of each tree was measured automatically during two days of each month by means of portable infrared gas analysers (Li-Cor 6200, USA and portable IRGA Walz, Germany) connected to one to eight assimilation chambers (5 l volume, Krüger GmbH, Germany) allowing parallel measurements of leaves of different age and light exposition according to the distribution of sun, shade, young, mature, and old leaves in the crown. The measurements were carried out automatically within three-minute-intervals and were made every 20 minutes during 48 hours. The temperature and the humidity of the air was measured inside and outside the assimilate chambers in one-minute-intervals by means of testostor 175 temperature and air humidity loggers (Testo GmbH, Germany). The photoactive radiation (PAR) was also monitored automatically in one-minute- intervals above and below the assimilation chambers by means of PAR sensors (UP GmbH, Germany) during the period of gas exchange measurements. The net photosynthesis per time unit was described on a leaf area basis in $\mu mol\ CO_2\ m^{-2}\ s^{-1}$. The area of the leaves was measured after the gas exchange measurements by means of an optical area meter (LI-Cor, USA). As to study the relationship of net photosynthesis and biomass production on an one-month-scale the gas exchange and biomass data were transformed into glucose units.

*Determination of soluble carbohydrates and starch*

Samples of young, mature, and old leaves, of the secondary phloem and xylem of branches, stem and roots (extracted with mini increment borers with a diameter of 1.4 mm, Bäucker et al. 1998), and fine roots of the three experimental trees of each species were collected monthly in the field. The freeze-dried samples were milled (corn size 0.08 mm) for the subsequent extraction of soluble carbohydrates and hydrolyses of starch. The content of the soluble carbohydrates glucose, fructose, sucrose, raffinose, and stachyose was investigated according to Puls and Rademacher (1986) by a sugar analyser after methanol/water extraction (3:1) and subsequent enzymatic hydrolysis of the starch (0.05% amylase, 0.05 % amyloglucosidase in ammonium acetate (pH 6). The total content of soluble carbohydrates and starch within the whole tree was calculated from the carbohydrate content in the tree fractions mentioned above and the corresponding biomass.

*Determination of protein*

The protein content of corresponding tissue samples collected for the analyses of soluble carbohydrates and starch was quantified according to a method described by Sauter et al. 1989 and Harms and Sauter (1992). Freeze-dried and milled samples were used for protein extraction with a Laemmli buffer solution containing 1 % mercaptoethanol. The proteins were precipitated with acetone and analysed using the Lowry method. The total protein content of the trees was also calculated from the protein content in the tree fractions and the corresponding biomass.

*Calculation of the respiration of the tree*

The respiration of the trees for the maintenance of cell functions and for growth was calculated for monthly intervals as the difference between the net photosynthesis, the biomass production and the storage/mobilisation of food reserves. For the three *Meliaceae* species investigated in this study soluble carbohydrates, starch, and proteins are the major food reserves (Gottwald 1961, Wu and Hao 1991). Lipids and other potential food reserves were not considered in this calculation.

*Statistics*

As to evaluate the statistical significance of the study the Gauß´ error of the investigation was calculated. Presented monthly values are means ± standard deviation of three trees and the monthly number of measurements carried out at each tree (net photosynthesis: n=1152, soluble carbohydrates and protein: n=10). The significance of the results was assessed by ANOVA at $p<0.05$ (*F*-test).

## Results

*Seasonal variation of net photosynthesis of Swietenia macrophylla, Carapa guinanesis, and Cedrela odorata*

During the one-year-experiment the mean daily light availability (6 a.m. until 6 p.m.) on the crown surface of the trees varied between 400 µmol $m^{-2}$ $s^{-1}$ during the wettest season (January until April) and 650 µmol $m^{-2}$ $s^{-1}$ from May until December. In 1999 the annual precipitation was approximately 20 % higher than the long-term mean annual precipitation of the study site.

In 1999 the mean net photosynthesis of *Swietenia, Carapa*, and *Cedrela* was 0.10, 0.78, and 0.28 µmol $m^{-2}$ $s^{-1}$, respectively (Fig. 1). Maximum photosynthesis at full sunlight of *Carapa* varied between 1.83 and 5.07 µmol $m^{-2}$ $s^{-1}$ and was also significantly higher compared to light saturated net photosynthesis of *Swietenia*, which was only 1.67 to 2.81 µmol $m^{-2}$ $s^{-1}$ and *Cedrela*, which was 0.15 to 3.94 µmol $m^{-2}$ $s^{-1}$. The annual course of the mean net photosynthesis of *Swietenia* and *Cedrela* was strongly correlated with the water supply. Highest rates of net photosynthesis were measured during the wet season from January until June, whereas at the beginning of the drier season the net photosynthesis decreased (Fig. 1). Seasonal fluctuations of the net photosynthesis of *Carapa* were less than of *Swietenia* and *Cedrela* (Fig. 1). In addition for *Carapa* the course of the photosynthesis during the year did not follow the course of the precipitation indicating a lower response of this species to changing soil water conditions compared to *Swietenia* and *Cedrela*. Comparing the net photosynthesis of *Carapa* with the soil water potential (Dünisch 2001) it became obvious that only water logged and extremely dry soils (soil water potential less than –500 hPa) caused a significant reduction of the net photosynthesis of this species.

*Seasonal changes in the carbohydrate and protein reserves of Swietenia macrophylla, Carapa guinanesis, and Cedrela odorata*

The soluble sugars glucose, fructose, and sucrose were present in *Swietenia, Carapa,* and *Cedrela* all year. In contrast raffinose and stachyose were found in *Swietenia* and *Cedrela* only during the drier season from August until November and in *Carapa* in March and April. Extractable proteins were found in all samples.

Seasonal changes of the monthly mean content of soluble carbohydrates and starch in *Swietenia* occurred simultaneously (Fig. 2a). The amount of soluble carbohydrates and starch increased in June. Maximum values were found in October and November. A significant decrease of the protein content of *Swietenia* was found in May, when only very small amounts of reserve carbohydrates were available.

A strong intra-annual oscillation of the monthly mean content of soluble sugars and starch was found in *Carapa* (Fig. 2b). A high content of soluble carbohydrates was found in January, May and June as well as from September until December. Highest starch

contents were found in March and April. Except in July and August low starch contents of *Carapa* were correlated with high amounts of soluble carbohydrates. In July and August the content of soluble carbohydrates as well as the starch content were low. The mean protein content of *Carapa* was 1.68 %. Differences between the monthly protein content of *Carapa* were not significant.

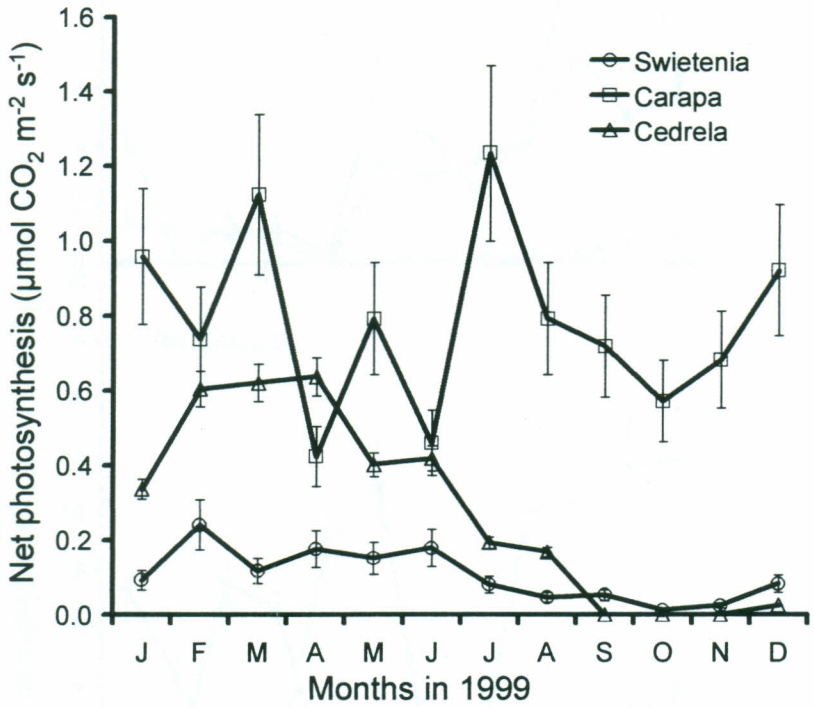


Fig. 1: Monthly mean net photosynthesis per leaf area and time [µmol $CO_2$ $m^{-2}$ $s^{-1}$] of 7-year-old *Swietenia macrophylla*, *Carapa guianensis*, and *Cedrela odorata*.

A third pattern of the seasonal course of food reserves was found in *Cedrela* (Fig. 2c). After a period with low contents of soluble carbohydrates and starch from January until May the content of soluble sugars increased from June until November followed by a strong decrease in December. After a simultaneous increase of the content of soluble sugars and starch in June the starch content already decreased in October indicating that the further increase of soluble sugars in October and November was due to the hydrolysis of starch. After the decrease of the content of reserve carbohydrates a significant increase of the mean protein content of *Cedrela* was found. This increase of the protein content was mainly due the budbreak of *Cedrela* in December and the high protein content of the new leaves.

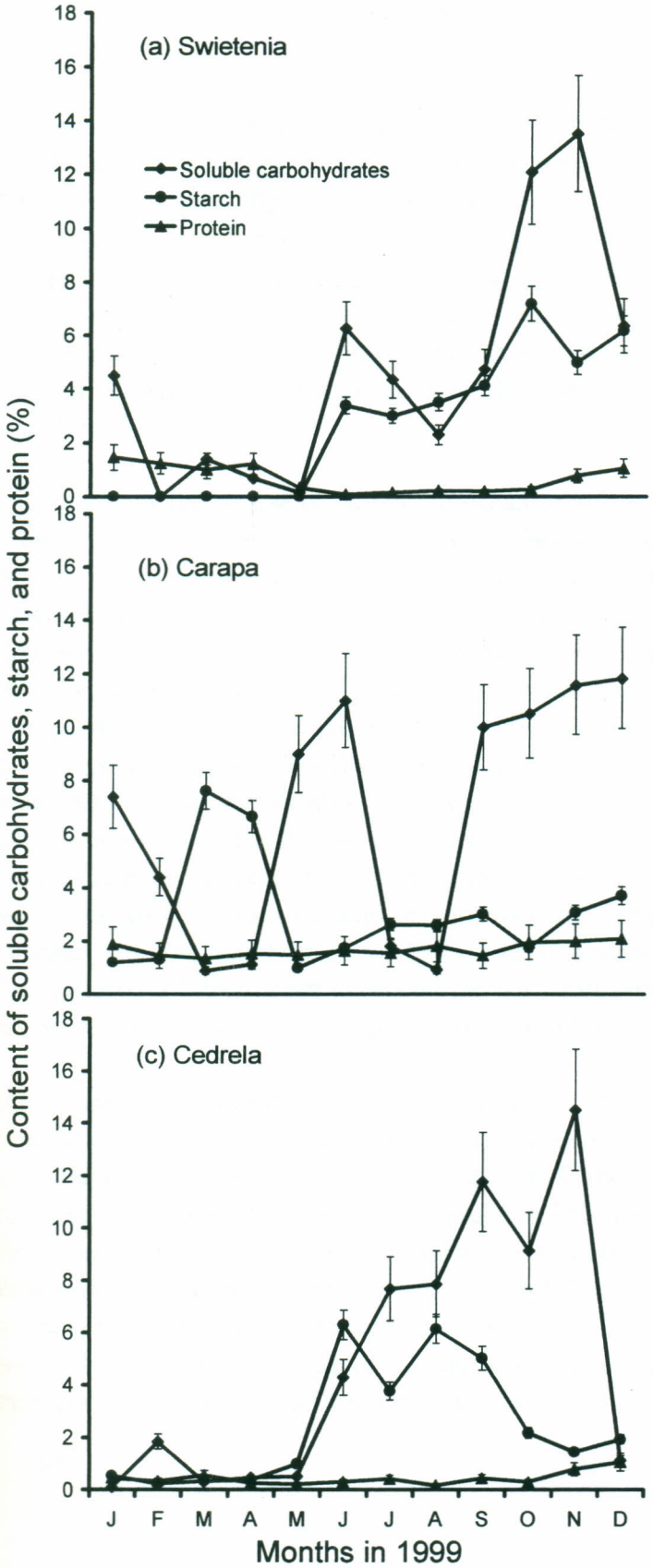


Fig. 2a-c: Monthly mean content of soluble carbohydrates (glucose, fructose, sucrose, raffinose, stachyose), starch, and protein [%] of 7-year-old (a) *Swietenia macrophylla*, (b) *Carapa guianensis*, and (c) *Cedrela odorata*.

*Seasonal pattern of assimilate allocation in Swietenia macrophylla, Carapa guianensis, and Cedrela odorata*

The annual biomass production of the 7-year-old *Swietenia, Carapa*, and *Cedrela* trees was 2.1 kg, 14.5 kg, and 5.4 kg representing a relative growth rate of 3.9 %, 13.7 %, and 8.8 %, respectively. Highest biomass production of *Swietenia* and *Cedrela* was found from December until April and from January until April, respectively, representing the wettest months of the study site (Fig. 3a and c). Growth dormancies of *Swietenia* and *Cedrela* trees were found from September until November and from October until December, respectively. In contrast high growth rates of *Carapa* were monitored from July until December, whereas short-term decreases of growth were found in April and in June (Fig. 3b).

As a tendency the course of biomass production of the three species followed the annual course of photosynthesis (Fig. 3a-c). Nevertheless it became obvious that in distinct phases of growth biomass production predominantly resulted from the mobilisation of food reserves. Mobilisation of food reserves was found in *Swietenia* especially in February and June, whereas in May and November a high portion of assimilates from photosynthesis was stored (Fig. 4a). A high mobilisation of food reserves was found in *Carapa* in February and in August before periods of reduced growth, whereas an increase of storage material was found in January and September (Fig. 4b). No correlation was found between the mobilisation and storage of carbohydrates and proteins, the net photosynthesis, and the biomass production of *Carapa*. Comparing the net photosynthesis, the alterations of the content of food reserves, and the biomass production of *Cedrela* it became obvious that the biomass production in January and February resulted mainly from the hydrolyses of reserve material (in January the biomass production of *Cedrela* even exceeded the net photosynthesis), whereas in December reserve carbohydrates were predominantly used for respiration (Fig. 4c).

During the experimental year 51 %, 42 %, and 55 % of the net photosynthesis of *Swietenia, Carapa*, and *Cedrela* were transformed into biomass (Fig. 3a-c), but a strong intra-annual variation of respiration losses was found within the year (Fig. 3a-c, Fig. 4a-c). High respiration of *Swietenia* was found in February, June, and November, in *Carapa* from January until August, and in *Cedrela* from February until May (Fig. 4a-c). Respiration of *Swietenia* and *Cedrela* was slightly correlated ($r^2$=0.27 and 0.31 respectively) with the storage and the mobilisation of carbohydrates and proteins (Fig. 4a and c). In contrast respiration of *Carapa* was not correlated with the seasonal changes in the carbohydrate and protein reserves as well as the biomass production (Fig. 4b).

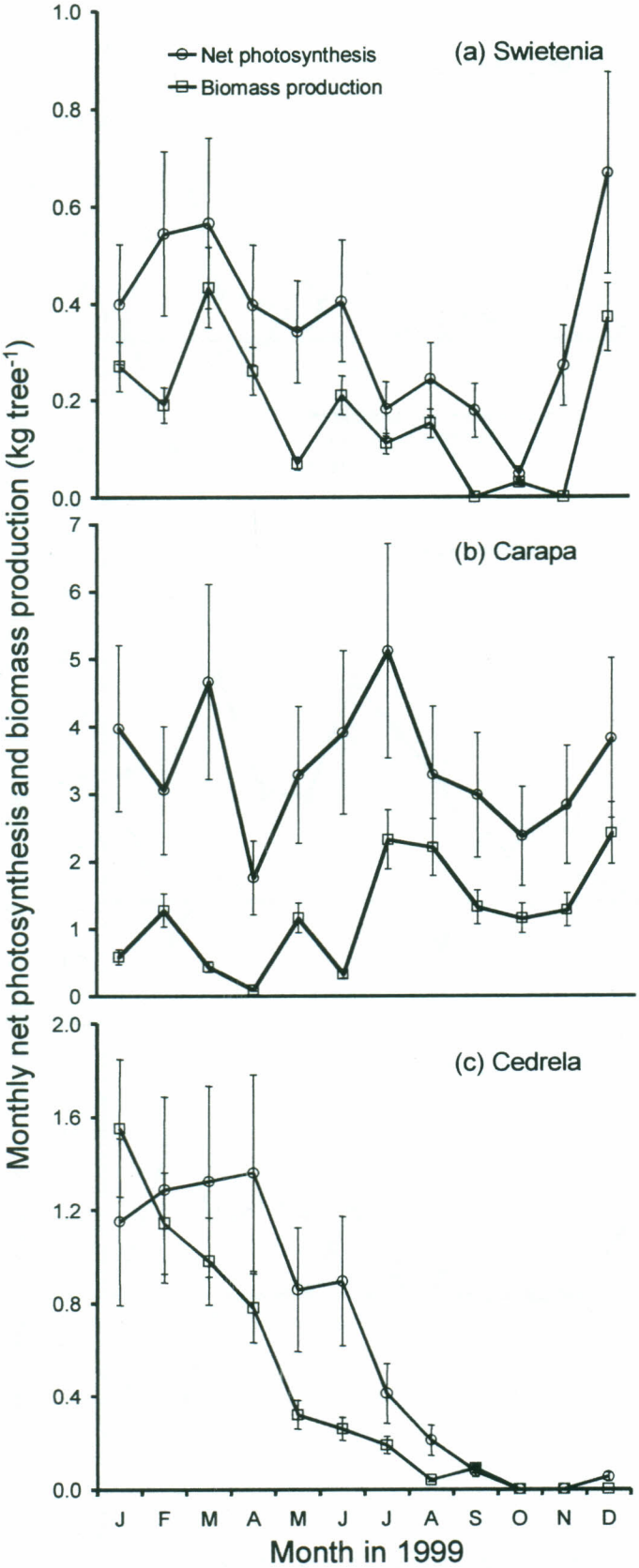


Fig. 3a-c:Monthly net photosynthesis (calculated as glucose) and biomass production per tree [kg] of 7-year-old (a) *Swietenia macrophylla*, (b) *Carapa guianensis*, and (c) *Cedrela odorata*.

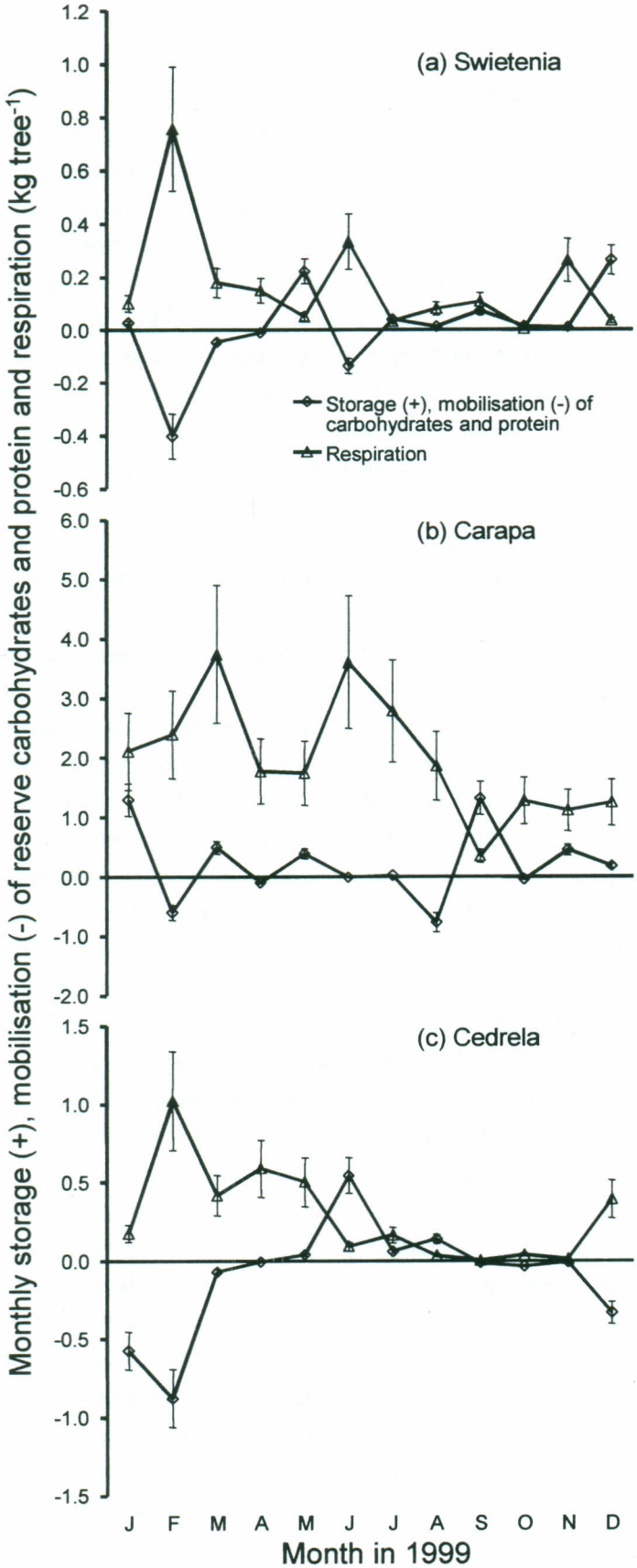


Fig. 4a-c: Monthly change of food reserves (soluble carbohydrates, starch, protein) and monthly respiration (calculated as glucose, [kg]) of 7-year-old (a) *Swietenia macrophylla*, (b) *Carapa guianensis*, and (c) *Cedrela odorata*.

## Discussion

Many field studies and investigations carried out under growth chamber conditions elucidated the endogenous (e.g. Zhang et al. 1994, Mitchell et al. 1999, Garcia-Plazaola 2000, Oleksyn et al. 2000) and exogenous influences on assimilate production, allocation and respiration of trees of temperate and boreal regions (Lange et al. 1971, Küppers et al. 1985, Dreyer et al. 1991, Reich et al. 1995), which allows the calculation of partial (Witowski 1997) and whole tree carbon balances (Larcher et al. 1973, Maurer and Matyssek 1997, Genard et al. 1998). Only few studies on assimilate production and allocation were carried out on trees from tropical regions (e.g. Küppers et al. 1986, Reich and Walters 1994, Pathre et al. 1998, Fernandez et al. 1999, Ishida et al. 1999). In our study the seasonal course of assimilate production, storage and mobilisation of three plantation-grown *Meliaceae* was studied with the aim to investigate the suitability of these species for cultivation in the Central Amazon. The investigations were carried out on an one-month-scale, running the risk of non detecting fast metabolic processes. Investigations carried out by Küppers et al. (1996, 1999) and Stegemann et al. (1999) showed that short-term changes of the light availability caused by light and sun flecks cause significant alterations of the photosynthesis. Similar effects can be expected from the light exposition of the leaves within the crown (Ishida et al. 1999). As to reduce this variation the study was carried out in an open plantation and on a study site which offers relative constant light conditions. To a certain degree a homogeneous light distribution was measured in the more transparent crown of *Swietenia* and *Cedrela*, whereas the dense crown and the hard to define leaf age of *Carapa* offered worse conditions for representative gas exchange measurements and sample collections. As to carry out the gas exchange measurements and the analyses of food reserves according to the stochiometric distribution of relevant tree fractions, the biomass distribution of each species was analysed at the beginning of the experiment (Schmidt et al. 1999, Dünisch and Schwarz 2001). The measurements and sample collections were carried out according to these partitioning. Nevertheless the high variation of photosynthesis between different leaf types caused a certain degree of uncertainty, which became obvious by the high standard deviation of the measurements (comp. Stockfors and Linder 1997). As shown by radioactive labelling of $CO_2$, transport, storage, and mobilisation of assimilates in trees are fast processes (Langenfeld-Heyser 1987, Blechschmidt-Schneider 1990, Hansen and Beck 1994), which last only some hours up to a few days and are enzymatically catalysed (Eklund and Little 1998). Studying the seasonal variation of photosynthesis and carbohydrate allocation on an one-month-scale these fluctuations are not detected and might be responsible for the weak correlation between the net photosynthesis, the storage and mobilisation of reserve carbohydrates and starch, and the respiration found in *Carapa guianensis.* Therefore for a deeper insight into the carbohydrate balance of the investigated *Meliaceae* labelling experiments under controlled conditions are recommended, as to calculate carbon fluxes in a higher resolution.

Comparing the net photosynthesis of the species measured in the field with measurements carried out under growth chamber conditions (Kriebitzsch et al. 2001), it became obvious that the plantation on the study site did not offer optimal conditions for assimilate

production of *Swietenia* and *Cedrela*, whereas *Carapa* is better adapted to the site conditions. During daytime the available light measured on the surface of the crown was close or even higher than the light saturation point of the species, but the recorded data did not give evidence for any light stress in *Swietenia* or *Cedrela*. The increase of the temperature due to the direct irradiation caused a dramatic increase of the leaf water potential of *Swietenia* and *Cedrela* (Dünisch unpublished data), which is responsible for a midday depression of photosynthesis as already discussed for other tree species by Tinoco-Ojanguren and Pearcy (1993), Pathre et al. (1998) and Wilson et al. (2000). Due to a lower sensitivity of *Carapa* leaves to high vapour saturation deficits photosynthesis of this species is less affected by high temperatures. This assumption is also confirmed by the strong correlation between the seasonal course of net photosynthesis of *Swietenia* and *Cedrela* and the precipitation on the study site, whereas no significant impact of a reduced precipitation on the net photosynthesis of *Carapa* was found. Although water deficits may play a role for the low net photosynthesis of *Swietenia* and *Cedrela* other exogenous factors seem to be of more importance, because the study was carried out during a year with high precipitation (approximately 3000 mm per year). Soil analyses carried out on the study site indicated that especially the low K, Mg, and S content of the soil (Schroth et al. 2000) might be responsible for the low net photosynthesis of *Swietenia* and *Cedrela* due to the significance of K and S for stomata regulation and enzyme reactions and of Mg for chlorophyll synthesis (Küppers et al. 1985, Marschner 1995). This assumption is also confirmed by investigations on the nutrient demand of these species showing a higher K demand of *Swietenia* and *Cedrela* for growth compared to *Carapa* (Mayhew and Netwton 1998, Schmidt et al. 1999, Dünisch and Schwarz 2001).

Following the annual course of growth and dormancy phases (Coster 1927, 1928, Sack 1998), the seasonal course of soluble carbohydrates and starch in *Swietenia* and *Cedrela* showed an annual pattern similar to annual patterns observed in gymnosperms and deciduous trees from temperate regions (Saranpää and Höll 1989, Fischer and Höll 1991, Harms and Sauter 1992, Sauter and Wellenkamp 1998). Comparing these findings with the onset of budbreak and the cambial growth of *Swietenia* and *Cedrela* (Coster 1927, 1928, Bauch and Dünisch 2000, Dünisch and Bauch 2001) the results indicate a high significance of pre-budbreak accumulation of soluble sugars and starch for the initial phase of the subsequent growth period. Due to the lack of new photosynthates in *Cedrela* during the dry season (deciduous species) budbreak and wood formation depends exclusively on the mobilisation of food reserves (comp. Gordon and Larson 1968). The own findings indicate that for new growth starch is hydrolysed first followed by the consumption of soluble sugars. In agreement with the high energy consumption for hydrolyses and transport of food reserves the respiration of *Cedrela* increased significantly during that period (Kozlowski et al. 1991, Mitchell et al. 1999), but the weak correlation between the seasonal variation of food reserves and respiration also showed that respiration is also strongly influenced by other factors (e.g. meteorological parameters). The seasonal course of reserve carbohydrates and protein found in *Swietenia* followed a similar pattern as found in gymnosperms of temperate regions (Ursino et al. 1968, Fischer and Höll 1991). This might be due to the semi-deciduous character of this species possessing photosynthesising tissue during the whole year. Gas

exchange measurements propose assimilate production also during the driest months (September to November) indicating an intact photosystem I and II (Tsel'niker and Chetverikov 1988). Accordingly to a certain amount the content of soluble carbohydrates might result from actual net photosynthesis, which might explain the unexpected simultaneous seasonal course of soluble sugars and starch concentration during this period. Nevertheless the actual net photosynthesis of September until November can not exclusively explain the increase of food reserves during this period, observed in *Swietenia*. Energy supply due to cyclic phosphorylation, other carbon sources (hemicelluloses, fructans) and $CO_2$ dark fixation might also contribute to the increase of reserves during this period. Although the photosystem I and II remains active all year in *Swietenia* the strong decrease of reserves at the beginning of the main growth period of this species indicates a portion of biomass production due to the mobilisation of reserves and a photosynthetic decline and pigment loss corresponding to foliar senescence found in temperate trees (Rosenthal and Camm 1997, Niinemets et al. 1999). In May the protein content of *Swietenia* decreased significantly. During this period only small amounts of reserve carbohydrates are available and a decrease of the net photosynthesis was found. Especially in tropical trees namely *Dalbergia odorifera* and *Meliaceae* species the function of vacuole proteins as reserves are discussed by Hao and Wu (1993) and Wu and Hao (1991). This possible transformation of proteins into carbohydrates, which predominantly only occurs during periods of a lack of carbohydrates gives further evidence for unfavourable conditions for the growth of *Swietenia* on the study site. *Carapa* is an evergreen species with no distinct annual growth characteristics (Vetter 1995, Bauch and Dünisch 2000). Consequently no annual course of net photosynthesis and the content of food reserves was found. The strong intra-annual oszillation of the content of soluble sugars and starch indicates a fast storage and mobilisation of food reserves in *Carapa* and a short-term adaptation to changing environmental conditions as well as a higher photosynthetic plasticity (Stegemann et al. 1999) compared to *Swietenia* and *Cedrela*. From own monthly data only assumptions on the carbohydrate cycle of *Carapa* can be made, whereas only flux measurements in a higher resolution could elucidate the relationship between assimilate production, storage and mobilisation. The constant protein content over the year indicates that proteins are not a major food reserve in *Carapa* or that under the given site conditions the mobilisation of proteins is not necessary for maintenance and growth respiration (Penning de Vries et al. 1974). Beside the seasonal course of biomass production secondary changes, especially heartwood formation have a strong influence on the seasonal course of reserve carbohydrates and proteins (Saranpää and Höll 1989, Magel et al. 1994). Only few information on heartwood formation of the investigated *Meliaceae* are available and seasonal patterns are completely unknown. Although heartwood formation was already induced in the 7-year-old *Swietenia, Carapa*, and *Cedrela* trees, fluctuations caused by these physiological processes were not considered in our study and need investigations in more detail as to get a better insight into the seasonal course of reserves.

The 7-year-old *Swietenia* and *Cedrela* trees showed a low biomass production compared to *Carapa*. Calculating relative growth rates (Ingestad 1987) for the life-span of the trees it became obvious that the experimental *Swietenia* and *Cedrela* trees already entered a phase of growth depression, whereas *Carapa* still showed sustainable growth (Azevedo

et al. 1999, Dünisch and Schwarz 2001). As a consequence it has to be taken into account that the carbohydrate balance was calculated for tree species of different vitality and therefore have to be considered as a case study. Changing site conditions may lead to different results. Especially the insufficient nutrient supply of *Swietenia* and *Cedrela* might have a significant impact on the carbon balance of these two species (Reid et al. 1983, Küppers et al. 1985, Bauer et al. 1991, Mc Donald et al. 1992). Therefore the lower respiration rate of *Swietenia* and *Cedrela* (49 % and 45 % of the net photosynthesis, respectively) compared to *Carapa* (58 % of the net photosynthesis) might be due to intrinsic factors causing a higher photosynthesis use efficiency or due to an insufficient assimilate supply favouring a direct pathway of assimilate allocation directly from the source to the sink (Hansen and Beck 1994). Studying the energy balance of assimilate storage, mobilisation and respiration especially under stress conditions a direct assimilate allocation is likely (Gravatt et al. 1998). On the other hand *Swietenia* and *Cedrela* show more regular growth dynamics compared to *Carapa*, which is predominately correlated with the water supply on the study site. Consequently the respiration increased in phases of the mobilisation of food reserves for the initiation of new growth, whereas under favourable site conditions growth is predominantly due to a direct assimilate allocation from the actual photosynthesis. The growth dynamics of *Carapa* did not show this annual cycle and remained less influenced by changing water conditions (Dünisch 2001). Therefore the permanent synthesis and mobilisation of reserve material all year might be a strategy of *Carapa* for fast adaptation to changing exogenous input although this pathway is more energy consuming (Grime 1979). Due to an extremely high photosynthetic capacity and a low light, water, and nutrient demand of *Carapa* for photosynthesis (Kriebitzsch et al. 2001) on this anthropogenuously influenced study site this pathway of carbon allocation is more successful in the long run than the more efficient direct biomass production from the actual net photosynthesis predominately observed in *Swietenia* and *Cedrela* after budbreak.

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## 2.2.1. Regulation of xylem sap flow in an evergreen, a semi-deciduous and a deciduous *Meliaceae* species in the Amazon

### Introduction

With regard to the global water balance and the water supply of large regions of South America the Amazon basin is considered as an important ecosystem, containing approximately 20% of the fresh water stocks of the earth (Marques et al. 1977, Franken and Leopold 1984, Leopoldo et 1987, Lesack 1993). Because of high deforestation due to extensive landuse systems (e.g. slash and burn management for agriculture) and logging activities during the last years special attend was given to the impact of deforestation of tropical rainforests on the water budget of the region (Hodnett et al. 1996). In this context it was of main interest in how far plantations for food and wood production can substitute extensive land use systems and in how far plantations can contribute to the stabilisation of the local water balance. Comparative studies carried out in primary forests and in plantations showed significant alterations of the water fluxes in plantations compared to natural sites indicating that sound information on the tree water use is needed as to select suitable species for timber production in plantations and for comparison of water balances of plantations and primary forests in scaling up approaches (comp. Tenhunen et al. 1998, Schroth et al. 1999). Although during the last years estimates of water use of tropical tree species became more numerous, for most of the economically important timber species of the Amazon information on the relationship of water supply, water uptake, xylem water fluxes and transpiration are missing.

Due to the development of inexpensive methods and a high applicability in the field whole tree water use is often studied by xylem sap flow measurements (Granier 1985, 1987, Schulze et al. 1985, Kostner et al al. 1995, 1998, Oren et al. 1998), which – on a daily scale – are strongly correlated with the transpiration of the tree. However, within the continuum soil-plant-atmosphere the xylem sap flow is regulated by the tree indicating apparent limitations studying the physiological regulation of water use of different species and the adaptation of diverse species to a changing water supply only by means of xylem sap flow measurements (Wullschleger 1998). Beside the regulation of the leaf area by leaf formation and litter fall, sapwood senescence (Granier et al. 1994, Philips et al. 1996, Wullschleger and King 2000), stomata regulation (Pearcy et al. 1989, Jones and Sutherland 1991, Fest et al. 1997, Irvine et al. 1998, Sparks and Black 1999, Busch and Losch 1999), osmoregulation (Balling and Zimmermann 1990, Marshal and Gircesa 1997), and the use of water storage compartments in the roots, in the stem, and in the branches are principal regulation mechanisms for the xylem sap flow of a tree (Herzog et al. 1995, Goldstein et al. 1998). This internal regulation causes non linear relationships and time delays between the sap flow measured in the xylem and the transpiration from the leaves. Sap flow measurements integrate different biophysical and physiological processes, which have to be studied separately as to evaluate plant – water relationships.

As to understand the relationship of xylem sap flow and the water supply of three high quality timber species from the Amazon in this study the significance of stomata opening

and closure, of the osmotic potential of paratracheal parenchyma cells of the xylem, and of the stem water storage on the diurnal and seasonal course of xylem sap flow of an evergreen (*Carapa guianensis* Aubl.), a semideciduous (*Swietenia macrophylla* King), and a deciduous (*Cedrela odorata* L.) *Meliaceae* species of the Amazon was investigated. The study was carried out with special regard to the adaptation of the species to a reduced water supply.

## Material and Methods

### *Study site and experimental trees*

The study was carried out from December 1997 until February 1999 in a plantation of 20 native and exotic timber species (100 planted trees each, spacing 3 m x 3 m) installed in January 1992 on the research station of the EMBRAPA Amazônia Ocidental, 29 km out of the city of Manaus, 3°8' S, 59°52'W (comp. Bauch et al. 1999). In particular species of the family *Meliaceae* were considered. The area is located at approximately 50 m above sea level with an annual precipitation of about 2,500 mm (Min. 110 mm (August) / Max. 295 mm (February) per month), a mean air temperature of 26.4° C, and a mean humidity of the air of 87 %. According to categorisation, the soil is a poor xanthic Ferralsol (FAO, 1990 with a low cation exchange capacity, Dünisch et al. 2000, Schroth et al., 2000).

For the study 3 trees each of *Carapa guianensis* Aubl. (evergreen species), *Swietenia macrophylla* King (semi-deciduous species), and *Cedrela odorata* L. (deciduous species) were selected (Table 1). From continuous observations and litter fall collectors installed under the trees it was calculated that the litterfall of *Carapa* is distributed over the year, whereas the *Swietenia* trees lost 26 % to 41 % of their total leaf biomass during the drier season from July until November 1998 and complete leaf loss of *Cedrela* was observed from August until November 1998 (comp. Dünisch and Schwarz 2001). The life cycle of *Carapa* leaves varied between 2 and 3 years, whereas the life cycle of *Swietenia* leaves was 13 to 20 month and of *Cedrela* approximately 9 to 11 months. Budbreak of *Cedrela* exclusively occurred at the beginning of December 1998, whereas budbreak of *Swietenia* and *Carapa* was also monitored from January until June 1998. As it was shown by monthly investigations presented elsewhere (Dunisch and Schwarz 2001) that during the 13 months of experiments the fine root biomass (Ø < 2 mm) of *Carapa* varied ± 7 %, of *Swietenia* ± 13 %, and of *Cedrela* ± 17 %, but no clear seasonal pattern became obvious. At the end of the experiments in February 1999 all trees were harvested and the biomass of different tree fractions was quantified. Although all trees showed comparable height and stem diameter the biomass of *Carapa* exceeded the biomass of *Swietenia* and *Cedrela* significantly (Table 1, comp. Dünisch and Schwarz 2001). The higher biomass of *Carapa* compared to *Swietenia* and *Cedrela* was predominantly due to a higher leaf and root mass of this species.

Table 1: Total tree height [m], stem diameter [cm], and biomass of leaves, stem/branches, and roots [kg] of the experimental *Carapa, Swietenia*, and *Cedrela* trees at the end of the experiments in February 1999 and leaf loss of the trees during the dry season from August until November 1998 [% of total leaf biomass].

| Experimental tree | Height (m) | Diameter (1.3 m) (cm) | Biomass (Leaves, Stem/Branches, Roots) (kg) | Leaf loss (dry season 1998) (% total leaf biomass) |
|---|---|---|---|---|
| Carapa 1 | 10.3 | 7.3 | 106 (26.9, 47.3, 31.8) | 4 |
| Carapa 2 | 8.5 | 7.9 | 104 (31.4, 43.3, 29.3) | 3 |
| Carapa 3 | 7.9 | 7.4 | 84 (26.7, 31.9, 25.4) | 4 |
| Swietenia 1 | 8.4 | 7.1 | 53 (4.2, 39.2, 9.6) | 26 |
| Swietenia 2 | 10.2 | 7.4 | 59 (4.9, 41.7, 12.4) | 41 |
| Swietenia 3 | 8.7 | 7.0 | 55 (3.9, 37.9, 13.2) | 37 |
| Cedrela 1 | 9.2 | 7.8 | 61 (7.3, 28.1, 25.6) | 100 |
| Cedrela 2 | 7.6 | 7.2 | 54 (6.0, 31.2, 17.8) | 100 |
| Cedrela 3 | 8.9 | 7.7 | 62 (7.0, 37.7, 17.3) | 100 |

Following the annual course of climatic characteristics on the study site (Leopoldo et al. 1987) in our study special regard was given to the regulation of the xylem sap flow of *Carapa*, *Swietenia*, and *Cedrela* during 5 periods:

(1) The wettest period (water logged soils and low differences between the day and the night vapour saturation deficit of the air, February/March 1998).
(2) A shortterm drier period during the wet season (drier soil, but low differences between day and night vapour saturation deficit of the air, end of April 1998).
(3) The end of the wet season (decrease of the soil water content and increase of the vapour saturation deficit of the air during daytime, July 1998).
(4) The driest season (low soil water content, high vapour saturation deficit of the air during daytime, September/October 1998).
(5) The end of the dry season/beginning of the wet season (increasing soil water content, decreasing vapour saturation deficit of the air during daytime, December 1998).

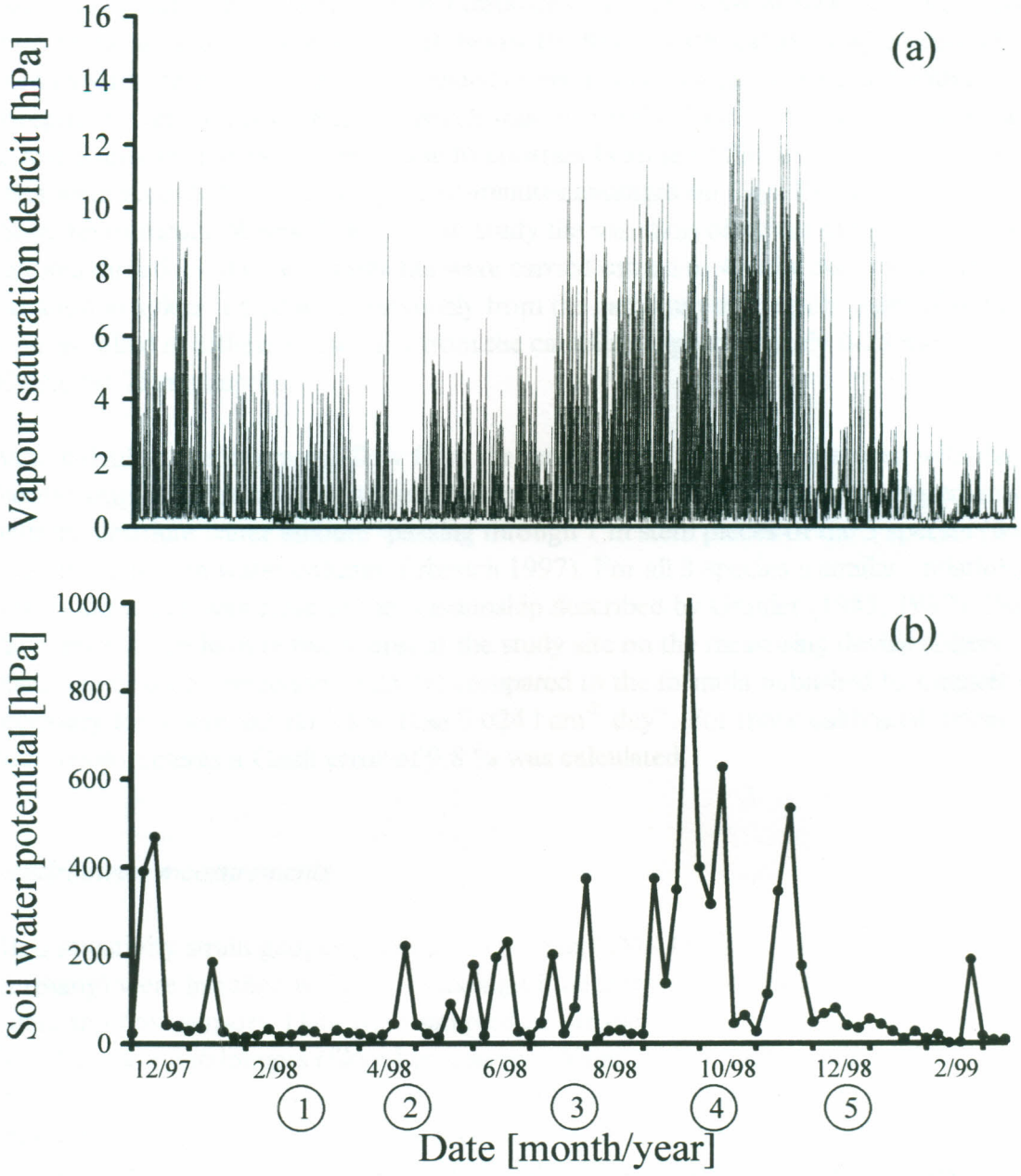


Fig. 1 a/b: (a) Vapour saturation deficit [hPa] measured on the crown surface of the experimental trees and (b) soil water potential of the plantation in a soil depth of 20 cm [hPa] during the period of experiments from December 1997 until February, 1999. The 5 experimental periods considered in this study are marked on the x-axis (❶ - ❺).

*Xylem sap flow measurements*

Xylem sap flow measurements were carried out according to Granier (1985, 1987) with a constant heat flow method using heated and unheated thermocouples (UP GmbH, Osnabruck, Germany ) installed with a distance of 12 cm between each other in a main root, at the stem basis (height 50 cm), below the first branch and at a major branch of each experimental tree. The upper (heated) sensor was continuously heated with a constant power supply (156 mW), which was switched off for 10 minutes every week as to avoid longterm artificial trends due to constant heating of the sensors (Eilers 2000). Data were recorded continuously as 10-minutes averages on Skye Datahog dataloggers (Skye Instruments, Wales, U.K.). As to study the variation of xylem sap flow in the 4 cardinal directions the measurements were carried out up to 4 radii. As to study the radial variation in xylem sap flow continuously from the cambium to the pith, pairs of sensors were installed in different distances from the cambium (approximately 0-25 mm, 25-50mm, 50-75mm depths).

As to calculate the xylem sap flow from the temperature gradients measured with the thermocouples the measuring system was calibrated correlating temperature gradients with the absolute water amount passing through 1 m stem pieces of the 3 species (water pressure: 1 to 5 m water column, Erbreich 1997). For all 3 species a similar relationship was found which was close to the relationship described by Granier (1985, 1987). Due to the impact of the high temperatures at the study site on the measuring device (Eilers 2000) major data correction (> 25 %) compared to the formula published by Granier was necessary for xylem sap flow less than 0.024 l $cm^{-2}$ $day^{-1}$. For those calibrated xylem sap flow measurements a Gauß error of 9.8 % was calculated.

*Dendrometer measurements*

High sensitivity strain gauges (accuracy 0.01 mm, DMS D6-UP GmbH, Osnabruck, Germany) were installed without wounding of the stem approximately 10 cm below the xylem sap flow sensors. Data were sampled automatically as 10-minutes averages on Skye Datahog dataloggers (Skye Instruments, Wales, U.K.). As to distinguish reversible changes in stem circumference from irreversible cambial cell divisions our data were filtered by linear regression analyses according to Dunisch and Bauch (1994). The daily change of the stem water storage was calculated from the difference between the daily maximum and minimum stem volume, which was calibrated against the shrinkage coefficients ("differentielles Quell- und Schwindmass") of corresponding phloem and xylem samples of the same trees.

*Wood anatomical characteristics and permeability of the xylem*

As to study the wood anatomical characteristics and the permeability of the xylem, discs were sampled at the end of the experiment at the height of xylem sap flow and dendrometer measurements. In all cardinal directions along the radius, blocks were used

to determine radial variation in percentage of cell type (vessels, fibres, axial and radial parenchyma) from cambium to pith. These data were obtained by means of an integration ocular lens and a counting instrument (Leucodiff, Boskamp). The variation of the individual vessel area was measured on amplified cross sections of 15 µm thickness (projection microscope Zeiss, Oberkochem, Germany) with a digitiser board (HIPAD Plus, Houston Instruments, Texas, U.S.A.). The density and the diameter of vessel pits (n = 150) were directly measured in the micrsocope with a measuring ocular lens on radial and tangential microtome sections of approximately 1 $cm^2$.

Photos (1:1) from the polished discs served for the determination of bark, sapwood, and heartwood portion by means of a digitiser board (HIPAD Plus, Houston Instruments, Texas, U.S.A.). The water conducting system of the secondary xylem was marked using 1 % methylenblue as a tracer. Xylem samples with a length of 3 cm were prepared with a drill (Ø 15 mm) continuously from the cambium to the pith. The dowel preparation was carried out under water as to avoid air embolism. The tracing was carried with a pressure of 10 cm water column for 5 minutes (Bauch 1964).

*Osmotic potential of xylem sap and xylem tissue*

As to quantify the osmotic potential of the xylem sap and the paratracheal parenchyma, xylem samples were collected monthly by means of an increment borer. Xylem sap was extracted out of the wood samples by means of a Scholander pressure chamber (SKPM 1400, Skye Instruments LTD., U.K.). Vessel with paratracheal parenchyma were separated from the xylem samples by micropreparation technique according to Dünisch et al. (1998). According to Lalk et al. (1992) sap of this tissue, which contains vessel sap and cytosol sap of parenchyma cells, was produced using mechanical pressure and ultra-high frequency treatments. The osmotic potential of these samples was measured by a Roebling osmometer. The contribution of different solutes to the cell osmotic pressure of the samples was calculated according to Bogeat-Triboulot and Levy (1998).

*Determination of soluble sugars*

The content of the soluble sugars (glucose, fructose, sucrose, raffinose, stachyose) of the monthly collected vessel sap and the vessel/paratracheal parenchyma tissue was analysed according to Puls and Rademacher (1986) with a sugar analyser. The content of soluble sugars in the sap samples was directly analysed after purification of the samples with a $C^{14}$-filter. The soluble sugars of the frozen dried tissue samples were extracted with methanol/water (3:1). Before analysis the extracts from the tissue samples were also purified ($C^{14}$-filtration).

*Quantitative subcellular element analysis*

Sample collection for the study of the distribution of mineral elements in the xylem of the experimental trees was also carried out monthly. Shock frozen xylem samples were embedded in Spurr's resin according to Kuhn et al. (1997) and semithin sections with a section thickness of 1 µm were prepared (LKB Historange). The distribution of elements with a "Ordnungszahl>8" within the xylem tissue was investigated quantitatively on a subcellular level by means of calibrated energy dispersive X-ray spectroscopy in combination with a transmission electron microscope (Philips EM 400 T, acceleration voltage 120 kV, spot size 0.3 µm; EDAX detector, running time 400 s, count rates of 1400 – 2000 cps with a dead time of 16 – 27 %) according to Dunisch et al. (1998). Calibrated quantitative subcellular K analyses were carried out with an error of 13 %.

*Infiltration of leaves*

For analyses of stomatal opening and closure a infiltration method described by Molisch (1912), Beyschlag and Pfanz (1990), and Küppers et al. (1999) was used. Sample collection of 5 mature sun-, half-shaded and shaded leaves each of all experimental trees was carried out at February 22, 1998, April 23, 1998, July 27, 1998, October 10, 1998, and Deceber 25, 1998 in 30 minutes intervals. After immediate determination of the fresh weight leaves were infiltrated with destilled water under vacuum. The infiltrated leaves were spread out between two glass plates and photographed against natural light. The portion of the infiltrated leaf area was analysed using a transparent integration sheet and a counting instrument.

*Statistical analyses*

As to evaluate the statistical significance of the study the Gauß´ error of every independant measurement (xylem sap flow, stomata opening, osmotic potential, sugar and subcellular element analyses, stem water storage) was calculated. The data were examined by analysis of variance (ANOVA) using the tree species and the 5 experimental periods (Fig. 1a/b) as variables. The significance of the results was tested for $P \leq 0.05$ by Fisher´s F-test.

## Results

### *Wood anatomical characteristics of Carapa guianensis, Swietenia macrophylla, and Cedrela odorata*

Tracer experiments showed that the xylem water conductance of all 3 species was restricted to the vessels. In the outer xylem of *Carapa* and *Swietenia* vessel distribution was diffuse porous (mean vessel diameter: 121 ± 37 µm and 113 ± 29 µm, respectively, whereas vessel size and distribution in the xylem of *Cedrela* showed half ring-porous characteristics (vessel diameter of vessels formed during the rainy season: 213 ± 21 µm, vessel diameter of vessels formed at the end of the rainy season in July: 78 ± 11 µm). Paratracheal parenchyma was present in the xylem of all 3 species, but most pronounced in the xylem of *Cedrela* formed at the beginning of the rainy season (period 1 and 5, Fig. 1 a/b) The mean vessel portion in the xylem of *Carapa* was 10 %, in the xylem of *Swietenia* 18 %, and in the xylem of *Cedrela* 7%. Light microscopical observations showed that the vessel lumen of the inner xylem of *Swietenia* and *Cedrela* was highly impregnated with accessory compounds indicating heartwood formation, whereas sapwood senescence and heartwood formation in the xylem of *Carapa* was more delayed.

### *Xylem sap flow of Carapa guianensis, Swietenia macrophylla, and Cedrela odorata*

Maximum total daily sap flow measured from December 1997 until February 1999 varied from 7 l $day^{-1}$ in *Swietenia*, the species with the lowest biomass to 16.4 l $day^{-1}$ in *Carapa*, the species with the highest biomass (Fig. 2, Table 1), Maximum 10-minutes average sap flow was found in the outer xylem of *Cedrela* (1.2 l $cm^{-2}$ $day^{-1}$) compared to 0.93 and 0.71 l $cm^{-2}$ $day^{-1}$, respectively in *Carapa* and *Swietenia*. Corresponding maximum sap flow velocities in the stem xylem of *Cedrela*, *Carapa*, and *Swietenia* are 7.03 m $h^{-1}$ , 3.69 m $h^{-1}$, and 1.67 m $h^{-1}$.
Xylem sap flow of *Carapa* was found over the total cross section of the stem, with a decrease of xylem sap flow from the outer xylem to the inner part of the stem of approximately 65 % (Fig. 2). Xylem sap flow of *Swietenia* and *Cedrela* was restricted to the outer 25 mm and 50 mm of the stem radius, respectively, representing a conductive xylem of approximately 2 to 4 years in *Swietenia* and 4 to 5 years in *Cedrela* (comp. Dünisch and Bauch 2001). Xylem sap flow measured in the inner sapwood of *Cedrela* showed a significant time delay compared to the xylem sap flow measured in the outer sapwood, whereas xylem sap flow measured in different stem depths of *Carapa* showed parallel run (Fig. 2).

The xylem sap flow of the evergreen species (*Carapa guianensis*), the semi-deciduous species (*Swietenia macrophylla*) as well as the deciduous species (*Cedrela odorata*) showed seasonal pattern following the annual course of the water supply on the study site. Maximum xylem sap flow was found from December until April representing the wettest months on the study site. An extreme intra-diurnal variation of xylem sap flow became apparent from February until April, which was more pronounced in *Swietenia*

and *Cedrela* compared to *Carapa* (period 1 and 2, Fig. 2). Remarkable amounts of xylem water flux were still measured in *Carapa, Swietenia* and *Cedrela* during the driest period of the year (period 4, Fig. 2). During the driest period the total xylem sap flow of *Carapa* was 23 %, of *Swietenia* 34 % and of *Cedrela* 14 % of the maximum xylem sap flow measured during the wet season.

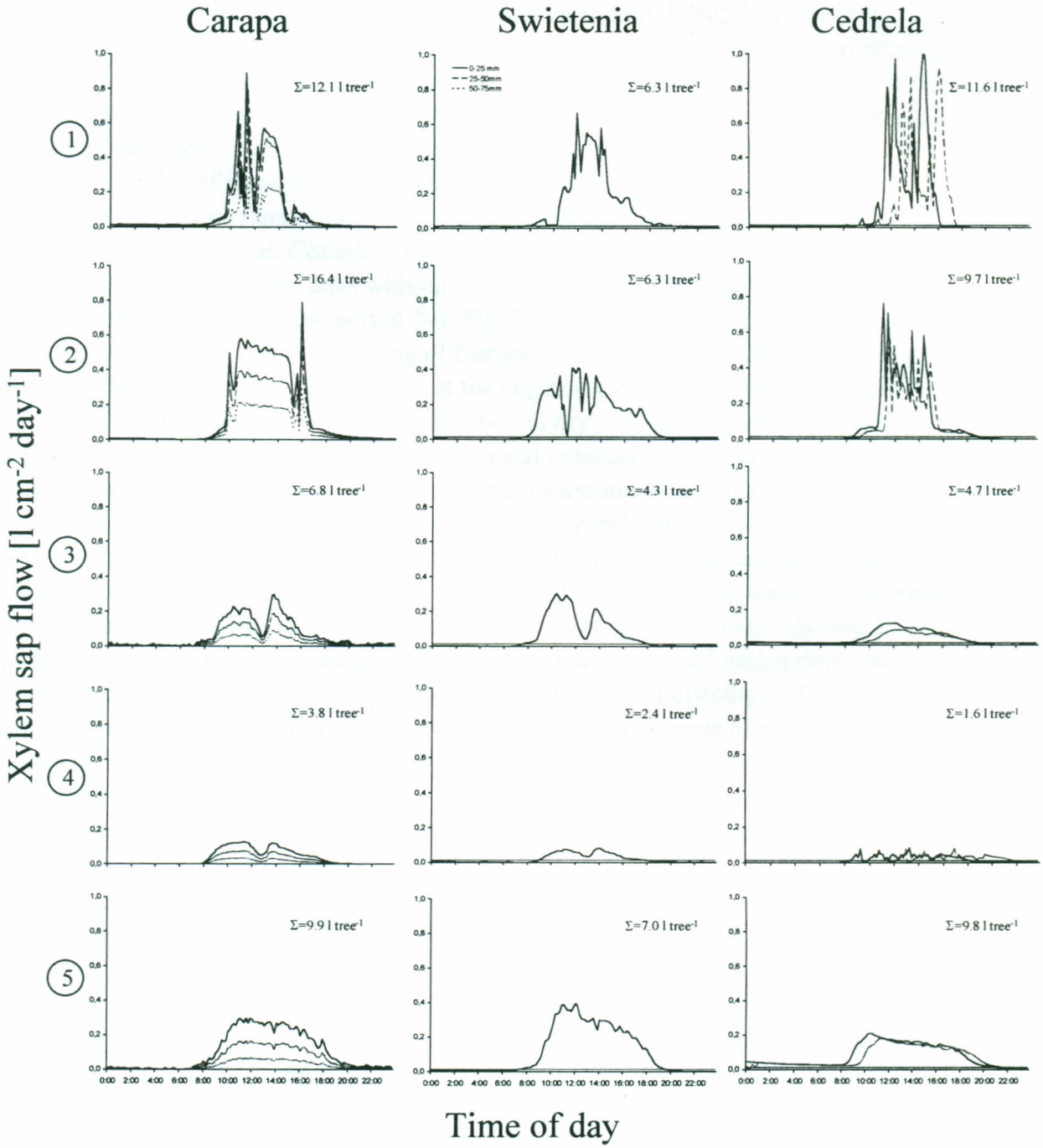


Fig. 2:Diurnal xylem sap flow of *Carapa, Swietenia*, and *Cedrela* [l $cm^{-2}$ $day^{-1}$] at 0.5 m stem height in a stem depth of approximately 0-25 mm, 25-50 mm, and 50-75 mm. Date of measurement: (1) February 22, 1998; (2) April 23, 1998; (3) July 27, 1998; (4) October 10, 1998; (5) December 25, 1998.

*Stomatal control of xylem sap flow of Carapa guianensis, Swietenia macrophylla, and Cedrela odorata*

Maximum stomata opening of the leaves studied by means of leaf infiltration experiments was highest in *Cedrela* and lowest in *Carapa*. Maximum stomata opening was correlated with the stomata density of the leaves of the 3 species (comp. Dünisch et al. 1999). Although the mean diurnal stomata opening of *Carapa, Swietenia*, and *Cedrela* showed a significant correlation with the total diurnal xylem sap flow of the trees (*Carapa* $r^2$ = 0.56, *Swietenia* $r^2$ = 0.87, *Cedrela* $r^2$ = 0.94) the diurnal variation of stomata opening and closure was not exclusively correlated with the xylem sap flow (Fig. 2, Fig. 3). A distinct time delay of a couple of minutes (branches of the upper crown) up to approximately 2 hours (stem basis) between the opening of stomata and the onset of xylem sap flow was found. Complete stomata opening was found in *Carapa* during the whole year (Fig. 3), whereas days without complete stomata opening were common in *Swietenia* during drier periods (period 2-4, Fig. 3) and in *Cedrela* before leaf loss (period 3, Fig. 3). A complete stomata opening of *Carapa, Swietenia*, and *Cedrela* leaves during the whole day was found in all 3 species at the beginning of the rainy season (period 5, Fig. 3) and in addition in *Carapa* during short-term dry periods of the rainy season (period 2, Fig. 3), representing periods of high and constant xylem flux rates (Fig. 2, Fig. 3). Even on a 30-minutes scale a high intra-annual variation of stomata opening and closure became apparent in *Carapa, Swietenia*, and *Cedrela* in February and March 1998. A slight reduction of the water supply during the rainy season caused midday stomata closure in *Swietenia* and *Cedrela* (period 2, Fig. 3), whereas stomata opening of Carapa remained unaffected. In July the stomata opening of *Carapa* also showed a midday depression of approximately 2 hours, which was correlated with a decrease in xylem sap flow (Fig. 2, Fig. 3). During this period the stomata opening of *Swietenia* and *Cedrela* was significantly reduced after 10 a.m although an increase of xylem sap flow was found in the afternoon after a slight (*Cedrela*, Fig. 2) to strong (*Swietenia*, Fig. 2) midday decrease. During the driest period (period 4) the stomata of *Swietenia* remained almost completely closed, whereas the stomata of *Carapa* remained open for 2 to 4 hours daily.

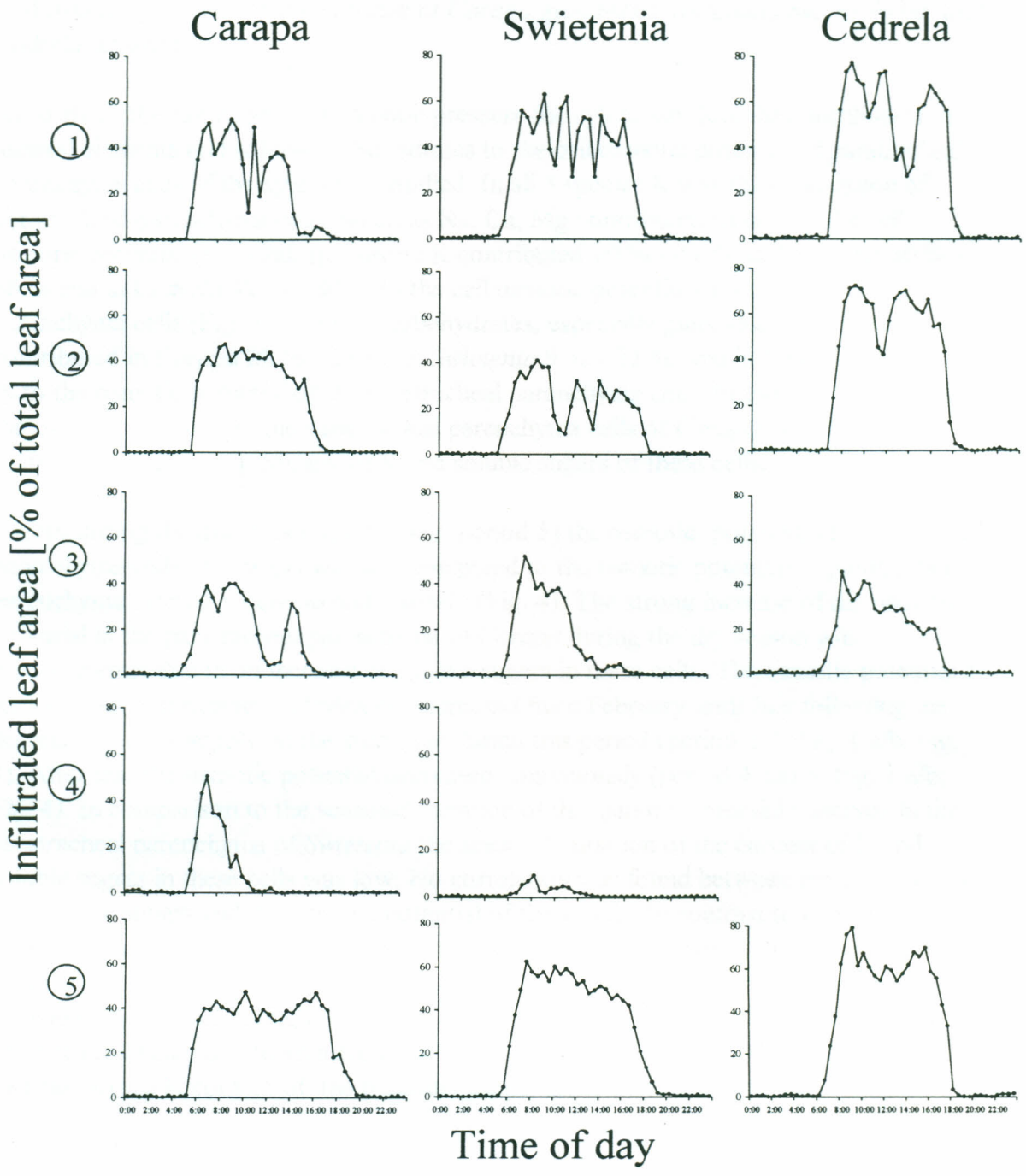


Fig. 3: Infiltrated leaf area of mature leaves of *Carapa, Swietenia*, and *Cedrela* [% of total leaf area] at (1) February 22, 1998; (2) April 23, 1998; (3) July 27, 1998; (4) October 10, 1998; (5) December 25, 1998.

*Cell osmotic pressure of xylem tissue of Carapa guinanesis, Swietenia macrophylla, and Cedrela odorata*

As to study the significance of osmotic pressure for xylem sap flow the contribution of mineral elements and soluble carbohydrates to the cell osmotic potential of paratracheal parenchyma cells of the xylem was studied. In all 3 species K was the main cation of paratracheal parenchyma cells, whereas Na, Ca, Mg contributed weakly to the cell osmotic potential (< 10 %). In *Carapa* K contributed 10 % - 47 %, in *Swietenia* 30 % - 66 % and in *Cedrela* 42 % - 80 % to the cell osmotic potential of the paratracheal parenchyma cells (Fig. 4). Soluble carbohydrates, especially glucose and fructose, contributed in *Carapa* 22 % - 61 %, in *Swietenia* 9 % - 22 %, and in *Cedrela* <1 % – 41 % to the osmotic potential of the paratracheal parenchyma cells. In total 60 % to 87 % of the osmotic potential of the paratracheal parenchyma cells of *Carapa, Swietenia*, and *Cedrela* was due to the content of K and soluble sugars of these cells.

Except during the driest month (October, period 5) the osmotic potential of paratracheal parenchyma cells of *Carapa* was low compared to the osmotic potential of paratracheal parenchyma cells of *Swietenia* and *Cedrela* (Fig. 4). The strong increase of the osmotic potential in the paratracheal parenchyma of *Carapa* during the dry season was predominantly due to an increase of soluble sugars in these cells. The osmotic potential of paratracheal parenchyma in *Swietenia* increased from February until July following the decreasing water supply on the study site during this period (period 1-3, Fig. 1 a/b, Fig. 4). After that the osmotic potential decreased continuously (period 4 and 5, Fig. 1 a/b, Fig. 4). In comparison to the seasonal variation of the osmotic potential observed in the paratracheal parenchyma of *Swietenia* the seasonal variation of the content of K and soluble sugars in these cells was low. No correlation was found between the content of K and soluble sugars and the osmotic potential of these cells. In contrast to *Carapa* and *Swietenia* the osmotic potential of paratracheal parenchyma in the xylem of *Cedrela* was positively correlated with the xylem sap flow (Fig. 2, Fig. 4). High osmotic pressure of the parenchyma cells during the wettest months (February until April, period 1 and 2) was predominantly due to an increase of soluble sugars, whereas a low intra-annual variation of the K content of the paratracheal parenchyma was found (Fig. 4).

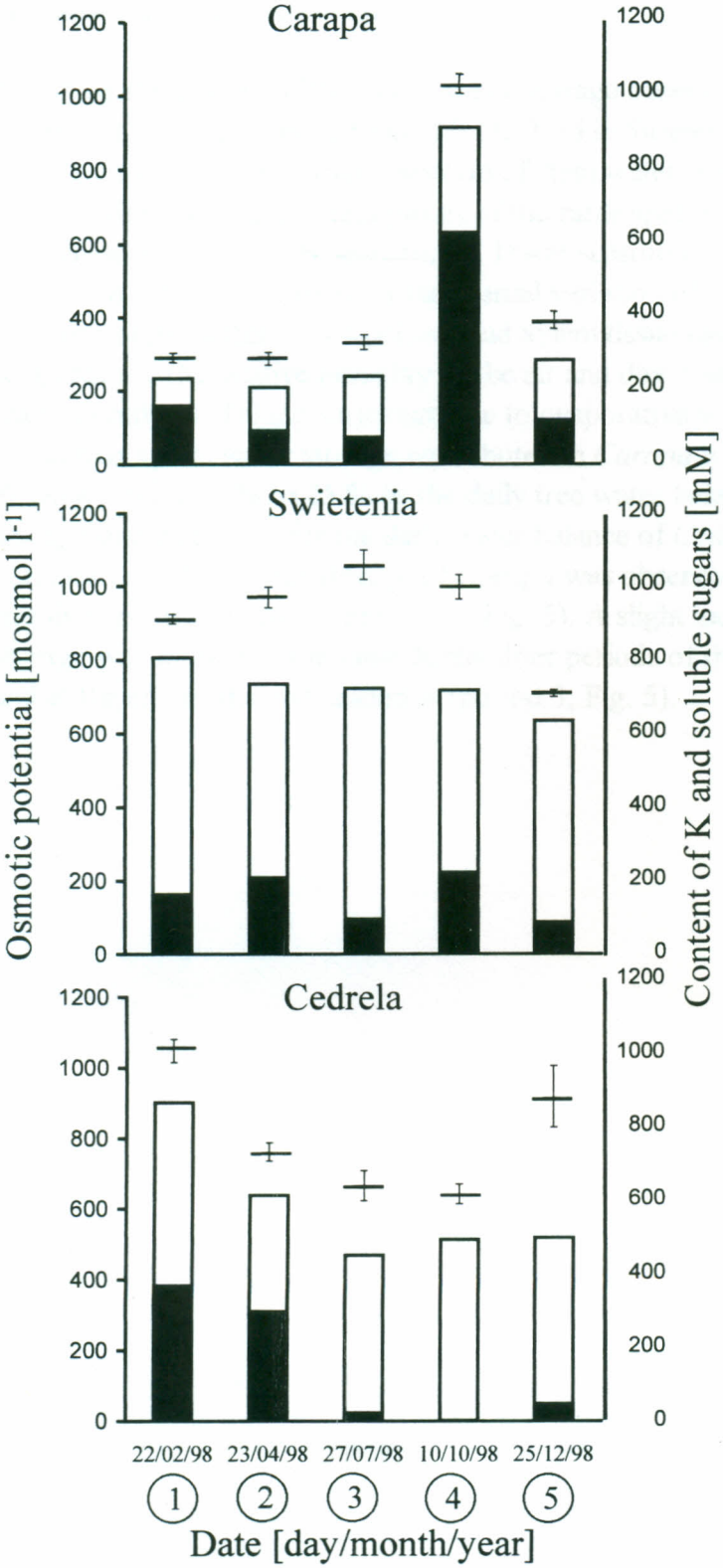


Fig. 4: Osmotic potential [mosmol $l^{-1}$] and content of (□) K and (■) soluble sugars (glucose, fructose, sucrose, raffinose, stachyose) [mM] of paratracheal parenchyma of *Carapa*, *Swietenia*, and *Cedrela* at (1) February 22, 1998; (2) April 23, 1998; (3) July 27, 1998; (4) October 10, 1998; (5) December 25, 1998.

*Diurnal changes of the xylem water storage of Carapa guinanesis, Swietenia macrophylla, and Cedrela odorata*

The diurnal variation of the xylem water storage observed in the 7-year-old trees varied between 1.7 l to 2.5 l in *Carapa*, 0.9 l to 1.3 l in *Swietenia*, and 0.6 l to 1.2 l in *Cedrela* (Fig. 5). Studying the diurnal variation of stem water storage of the trees in comparison to the shrinkage of fresh stem pieces of the same species it became obvious that 0.2 l (wet season) to 0.5 l (dry season), 0.1 l (wet season) to 0.4 l (dry season), and 0.5 l (wet season) to 1.5 l (dry season) of the diurnal variation of the xylem water storage are due to hygroscopic shrinkage of phloem and xylem tissue caused by diurnal changes of the temperature, the relative humidity of the air and direct water contact of the tree surface (rain, stemflow). Taking shrinkage due to evaporative water loss into consideration it was found that xylem water storage contributed in *Carapa* with 14 % to 35 % and in *Swietenia* with 13 % to 25 % to the daily tree water balance, whereas xylem water storage was negligible for the daily water balance of *Cedrela* (Fig. 5). High diurnal variation of xylem water storage of *Carapa* was observed in periods of changing water supply (period 2, 3, and 5, Fig, 1 a/b, Fig. 5). A slight increase of the use of xylem water storage was found in *Swietenia* during drier periods of the wet season (period 2, Fig. 4) and at the end of the wet season in (period 3, Fig. 5).

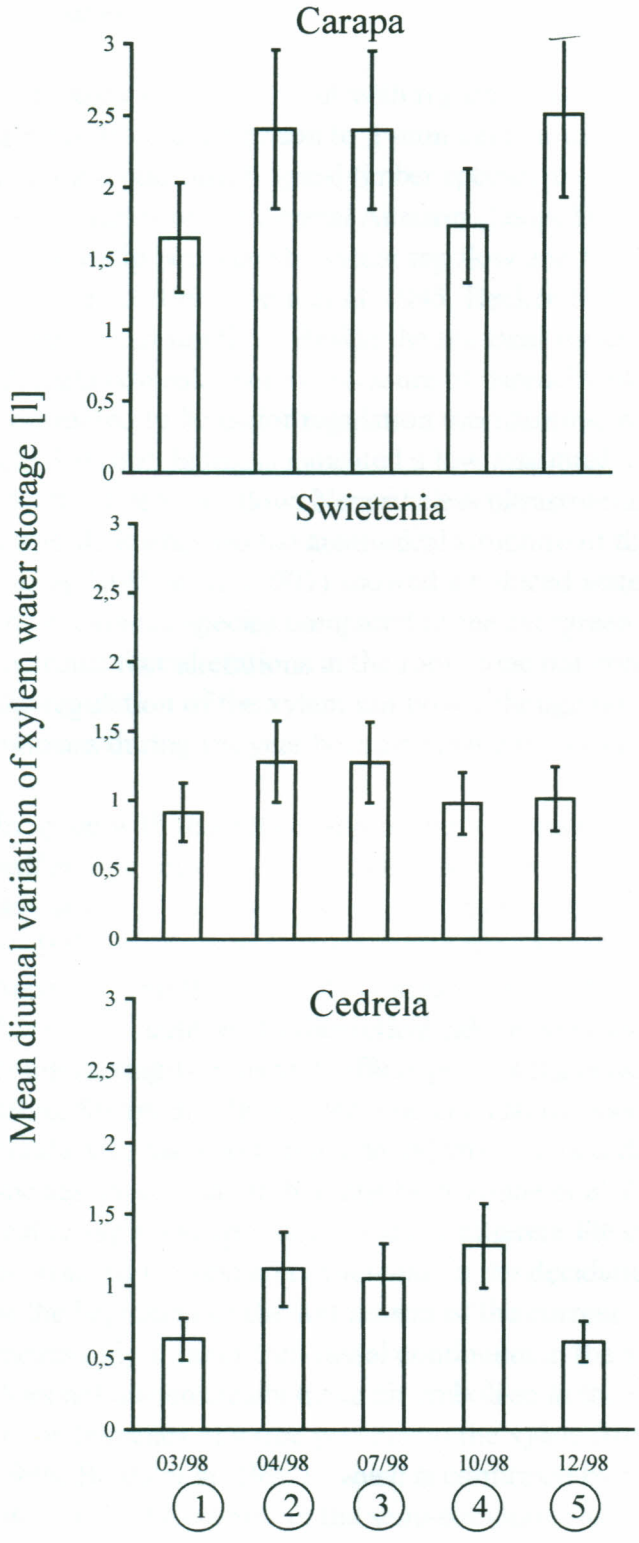


Fig. 5: Mean diurnal variation of xylem water storage [l] of *Carapa, Swietenia*, and *Cedrela* in (1) March 1998, (2) April 1998, (3) July 1998, (4) October 1998, and (5) December 1998.

## Discussion

This study was carried out with regard to the adaptation of an evergreen (*Carapa guianesis*) in comparison to a semi-deciduous (*Swietenia macrophylla*), and a deciduous (*Cedrela odorata*) tropical timber species to short-term and seasonal changes of the water supply of the Central Amazon (Leopoldo et al. 1987). Due to the strong relationship between the xylem sap flow and the water supply of a tree (Kramer 1985, Breda et al. 1993, Oren et al. 1995, Becker 1996) emphasis was given to the regulation of the xylem sap flow. Beside the seasonal variation of the leaf mass of the species stomata control, osmotic pressure of parenchyma cells, and the xylem water storage were considered to be major regulation mechanisms, whereas the low intra-annual variation of the fine root biomass indicated a low relationship between root formation, root death and the xylem sap flow. Nevertheless ultrastructural studies on the impact of nutrient and water deficiency on the anatomical structure of the fine roots of *Meliceae* species carried out by Noldt et al. (2001) showed a reduced water absorbency capacity of fine roots of the deciduous species compared to the evergreen species during drought periods. This indicates that alterations in the root zone not considered in this study can contribute to the regulation of the xylem sap flow although no significant changes of the fine root biomass during the year become apparent (comp. Lott.et al. 1996, Leuschner 1998).

In agree with theoretical approaches (Zimmermann and Brown 1971, Kramer 1985) the half ring-porous xylem structure and large size of vessels formed at the beginning of the wet season ("earlywood vessels") observed in the outer xylem of *Cedrela* (Tomaszelli et al. 1999, Dünisch and Bauch 2001) favoured the xylem sap flow expressed in terms of maximum sap flow velocity compared to the diffuse-porous species *Swietenia* and *Carapa.* In contrast to theoretical calculations and experimental studies carried out with conifers, ring-porous and diffuse-porous angiosperms (Vertessy et al. 1995, Phillips et al. 1996, Sperry and Ikeda 1997) no correlation was found between the vessel size, the conductive sapwood area, and xylem cavitation due to air embolism between the 3 species. According to findings by Andrade et al. (1998) this might be due to the different leaf to sapwood area ratios and the different life cycle of the leaves of the 3 species. In contrast to *Carapa* and *Swietenia*, in the deciduous species *Cedrela* all leaves are formed at the beginning of the wet season of the current year ("earlywood vessels"), which means only a direct leaf-vessel continuum in the xylem of the recent year. Annual leaf fall does not automatically mean air embolism in the older vessels due to anatomical barriers in the branches of a tree preventing the xylem from air embolism after leaf fall (Aloni et al 1996, Breda et al. 1999), which is confirmed by the high conductivity of the 2 to 4-year-old xylem of *Cedrela*. In the semi-deciduous and evergreen species vessels formed in former years are still directly connected to leaves formed during the last 2 to 3 years, raising the risk of air embolism in the older xylem due to the loss of stomata control in older leaves (Sperry 1986, Havanagh and Zaerrr 1997). In agreement with our findings due to the significance of K for stomata control this is especially expected on our study site, which is extremely poor in K (Schroth et al. 2000) and in *Swietenia*, which is high demanding in K (Schmidt et al. 1999, Dünisch and Schwarz 2001). Consequently complete loss of xylem conductivity became already apparent in the 3-year-old xylem of *Swietenia*, whereas sapwood senescence was more delayed in *Carapa*, which has a lower

K demand for tree growth. There was further evidence for the significance of the leaf to sapwood ratio and junction for radial xylem sap flow gradients by the distinct time delay between the xylem sap flow measured in the outer and in the inner sapwood of *Cedrela* in comparison to parallel xylem sap flow measured in the outer and inner sapwood of *Carapa.* The time delay between the outer and inner sapwood water flow in *Cedrela* might be due to a free water flow from the roots to the leaves exclusively in the outermost xylem, whereas water from the inner sapwood has to pass through vessel pits, which have a lower conductivity compared to the longitudinal vessel junctions. In contrast a higher portion of free xylem water flow in the vessel system can be assumed in *Carapa.*

Beside the seasonal course of the soil and atmosphere water potential on the study site, in the 3 tropical *Meliaceae* species stomata opening and closure was the major regulation mechanism for xylem sap flow, which is in agree with the cohesion theory (Böhm 1893, Zimmermann and Brown 1971). Beside water induced stomata regulation light induced stomata opening and closure has a significant influence on the xylem sap flow of the tree (Küppers et al. 1999). Beside the day and night cycle of stomata opening short-term changes of the light conditions caused by light- and sun-flecks cause non-uniform opening of the stomata, which causes a decrease in leaf conductance (Whitehead et al. 1981, Jones and Sutherland 1991, Granier et al. 1992, Phillips and Oren 1998). Our findings indicate that stomata opening and xylem sap flow of the 3 species are strongly influenced by fast changing light conditions during the wet season, which is the season of maximum water uptake. Due to the higher light demand of the photosystem I and II of *Swietenia* and *Cedrela* compared to *Carapa* (Kriebitzsch et al. 2000, Dünisch and Puls 2001) short-term periods of reduced light from January until May due to the change of sunny and cloudy periods causes stronger partial stomata closure in these species compared to *Carapa.* With regard to the pronounced dependency to maximum water and nutrient uptake during the wettest period a negative impact of stomata closure during this period to growth especially of *Swietenia* and *Cedrela* can be expected (Dunisch and Bauch 2001).

Studies on transpiration and xylem sap flow of tropical tree species (Jordan and Kline, 1977, Granier et al. 1992, Oren et al. 1995, Becker 1996) often indicate high xylem water flux, although the soil to atmosphere water potential in the humid tropics is lower than inmost of the temperate regions. Maximum xylem sap flow velocity of *Cedrela* exceeded most of the data published for trees of temperate regions (e.g. Baumgartner 1934, Granier et al. 1992, Breda 1993, Cienciela and Lindroth 1995), whereas xylem sap flow velocity of *Swietenia* and *Carapa* varied in the range reported for species from temperate regions. Some authors assumed an increase of xylem sap flow due to high osmotic pressure in parenchyma cells of trees from the humid tropics (Braun 1988, comp. Balling and Zimmermann 1990, White et al. 1996, Tschaplinski et al. 1998). High osmotic potentials found in the paratracheal parenchyma of *Cedrela* during the wet period (period of maximum sap flow) indicate a sink of paratracheal parenchyma to osmotic solutes during the main growth season as to obtain high osmotic pressure and xylem sap flow during a period of high soil water content, but low vapour saturation of the atmosphere (Fig. 1 a/b). In contrast to *Cedrela* high osmotic potentials were found in paratracheal

parenchyma cells of *Swietenia* and *Carapa* in periods of a decreasing water supply. This observation gives some evidence that osmotic pressure of paratracheal parenchyma is used in *Cedrela* as to maximise water uptake during periods, which offer the best conditions for the plant water supply, whereas osmotic pressure in paratracheal parenchyma of *Carapa* and *Swietenia* is used as to counteract a decreasing water availability. The permanent high osmotic potential of paratracheal parenchyma of *Swietenia* during the year indicate a general lake of water for the growth of *Swietenia* in the plantation under study (comp. Dünisch 2001). In contrast to *Carapa* and *Cedrela* an increase of the osmotic potential of paratracheal parenchyma of *Swietenia* was not due to an influx of K or soluble sugars assuming an influx of proteins (Sauter et al. 1989), which might indicate a lake of assimilates and nutrients (K, Na) in *Swietenia* for osmoregulation (Andrade et al. 1992, Jensen and Losch 1992, Stark 1992, Collet and Guehl 1997).

Xylem water storage was negligible for the xylem sap flow of *Cedrela*. In agree to other studies the absolute amount of xylem water storage in *Carapa* and *Swietenia* is only suitable for the compensation of short-term daily water deficits (Tyree and Yang 1990). Due to the reduced sapwood portion of *Swietenia* compared to *Carapa* the regulation capacity for the xylem sap flow of *Swietenia* by means of the use of xylem water storage is reduced compared to *Carapa* (Machado and Tyree 1994, Wullschleger et al. 1998). Nevertheless the significance of the xylem water storage for the plant-water relationship of *Swietenia* and *Carapa* should not be underestimated, because the study site offers good conditions for the refill of xylem water during night (vapour saturated atmosphere, Fig, 1 a) during most time of the year. This means that a portion 13 % to 35 % of the daily water balance of these two species can contribute to the annual water balance in the same order of magnitude. Beside a direct effect of the xylem water storage on the water supply of *Carapa* and *Cedrela* a positive influence of the use of xylem water storage on the photosynthesis due to prolonged daily stomata opening can be assumed in drier periods (Busch and Losch 1998, Arenda et al. 2000).

From these findings it can be concluded that the annual course of xylem sap flow of the deciduous species *Cedrela odorata* is strongly determined by genetic factors, maximising xylem sap flow during the period of best water supply by means of annual leaf formation, high xylem conductivity and osmotic pressure of paratracheal parenchyma during the wet period. The evergreen species *Carapa guianensis* and the semi-deciduous species *Swietenia macrophylla* have a lower capacity for high xylem sap flow compared to *Cedrela* and favour the compensation of a reduced water supply to a certain amount by means of stomata control, osmoregulation and the use of xylem water storage. In this context it turned out that *Carapa* is better adapted to drought conditions compared to *Swietenia*, which has to be considered for the cultivation of these high quality timber species in plantations.

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## 3. Cooperation and scientific exchange

Cooperation with SHIFT-project ENV 23:
Autecological investigations of Miconia sp. and Bellucia sp. are carried out in cooperation with the SHIFT-project ENV 23 (Dr. H. Preisinger) as to study the relationship between secondary tree species and the planted trees in the plantation systems.

Cooperation with the SHIFT-project ENV 45:
Element distribution in the rhizosphere of mixed plantations. Cooperation with the SHIFT-project ENV 45 (Dr. J. Lehmann). Unfortunately this study is delayed due to problems related to the import of embedding reagents.

Cooperation with SHIFT-project ENV 52:
Studies on the heartwood formation and durabilty of the wood from plantation and natural grown trees are carried out in cooperation with SHIFT project ENV 52. In this study the fauna of decomposed wood samples is identified in the scientific group of ENV 52.

Investigations on the litter decomposition in the plantation system II are carried out by the SHIFT-project ENV 52 (Prof. Dr. Beck, Dr. C. Martius, Dr. Höfer). Data on the water and mineral element supply in this plantation system are studied within the project ENV 42 and will be evaluated in cooperation with project ENV 52.

Cooperation with the SHIFT-project 102:
Allometric relationships between dendrometric parameters and the tree biomass of native species were developed in cooperation with the SHIFt project ENV 102.

Cooperation with the University of Paraná, Curitiba:
Chemical soil analyses and studies on the mineral nutrition of plantation grown *Ceiba pentandra* and *Virola surinamensis* are carried out in cooperation with Prof. Dr. B. Reissmann and Dr. E. Neves, University of Paraná. Sample collection and element analyses were carried out by Edinelson Neves (University of Parana), Oliver Dünisch and Thomas Schwarz (University of Hamburg).

Cooperation with the Institute of Wood Chemistry, Federal Research Center for Forestry and Forest Products, Hamburg:
Studies on the seasonal variation of the content of reserve carbohydrates of plantation grown trees are carried out in cooperation with Dr. J. Puls, Institute of Wood Chemistry, Federal Research Center for Forestry and Forest Products, Hamburg (comp. 2.3.).

Cooperation with the Institute of Forestry, Federal Research Center for Forestry and Forest Products, Hamburg:
Studies on the photosynthesis of *Cedrela odorata* L. are carried out under controlled conditions in coopertion with Dr. Kriebitzsch, Institute of World Forestry, Federal Research Center for Forestry and Forest Products, Hamburg.

Scientific exchange:

Research stay of Dr. E. Neves (EMBRAPA-CNPF, Curitiba) at the University of Hamburg (20.8.-10.9.2000)

Research stay of Dr. L. Gasparotto (EMBRAPA Amazonia Ocidental, Manaus) at the University of Hamburg (4.9.-10.9.2000)

Research stay of C. P. Azevedo (EMBRAPA Amazonia Ocidental, Manaus) at the University of Hamburg (4.9.-10.9.2000)

Research stay of R. R. Morais (EMBRAPA Amazonia Ocidental, Manaus) at the University of Hamburg (4.9.-10.9.2000)

## 4. Comparison of the investigations with the actual plan of the project

After six years of field and laboratory work the SHIFT-project ENV 42 is in the final phase and in the second half of 2000 special attention was given to data evaluation and the preparation of publications. Sound information on the relationship of light, water, nutrient supply and the growth of Swietenia, Carapa amnd Cedrela is already available. Corresponding results will be available for *Dipteryx* and *Hymenaea* as well at the end of the project in April 2001. In 2000 the investigations of the project were carried out according to the actual plan of the project.

The study on the water supply of the trees could be intensified in 2000 and these studies will continue also when the SHIFT project will have finished in 2001 (PhD thesis of Ronaldo Morais INPA/EMBRAPA/University of Hamburg).

First results were obtained from the provenance study installed in 1999. Results were presented at the workshop on neotropical ecosystems in Hamburg (4.-10.9.2000). See Proceedings of the Fourth SHIFT-Workshop, Hamburg, September 4-9, 2000.

Assessing wood quality of the plantation grown trees, the case study carried out for *Carpa guianensis* were extended to heartwood formation and the durabilty of the wood of *Swietenia, Cedrela, Dipteryx,* and *Hymenaea*. Results were presented at the workshop on neotropical ecosystems in Hamburg (4-10.9.2000). See Proceedings of the Fourth SHIFT-Workshop, Hamburg, September 4-9, 2000.

## 5. Relevant project publications and supplementary individual contributions

**Publications**

In 2000 research results were presented an the Conference on "Dendrochronology for the third millenium" held in Mendoza, Argentina (2.-7.4.2000), on the IUFRO World Congress in Kuala Lumpur, Malaysia (9.-14-8.2000), the workshop on "Neotropical Ecosystems" in Hamburg (4-10.9.2000) and the conference on "Agroforestry Systems" in Manaus (20.-24.11.2000).

**Relevant project Publications**


1. Bauch J., O. Dünisch (2000): Comparison of growth dynamics and wood characteristics of plantation-grown and primary forest *Carapa guianensis* in Central Amazonia. IAWA Journal 21, 321-333.

2. Dünisch O., J. Bauch, M. Müller, V.R. Montóia, L. Gasparotto (2000): Cambial growth dynamics and formation of increment zones in the xylem of *Swietenia macrophylla* King, *Carapa guianensis* Aubl. and *Cedrela odorata* L. Proceedings Dendrochronology for the third millenium, Mendoza, April 5-9, Argentina.

3. Dünisch O., J. Bauch, M. Müller, V.R. Montóia (2000): Exogenous influences on the cambial growth dynamics of plantation-grown *Swietenia macrophylla* King, *Carapa guianansis* Aubl., and *Cedrela odorata* L. Proceedings IUFRO World Congress, Kuala Lumpur, August 10-15, 2000, Malaysia.

4 Atayde C., M. Silva, O. Dünisch, C. Azevedo (2000): Wood anatomical and technological properties of *Hymenaea* sp. of plantation and natural grown trees. Proceedings of the Fourth SHIFT-Workshop, Hamburg, September 4-9, 2000.

5. Dünisch O., J. Bauch, L. Gasparotto, E. Neves, C. Azevedo, R. Morais (2000): Exogenous influences on the growth dynamcis of native timber trees of the Amazon. Proceedings of the Fourth SHIFT-Workshop, Hamburg, September 4-9, 2000.

6. Dünisch O., J. Bauch, T. Schwarz, J. Puls, V.R. Montóia (2000): Provenance study of native tree species of the Amazon for wood production in plantations on the „terra firme" near Manaus. Proceedings of the Fourth SHIFT-Workshop, Hamburg, September 4-9, 2000.

7. Dünisch O., J. Puls, S. Voiß, M. Reissen (2000): Seasonal variation of photosynthesis, reserve carbohydrates, and biomass production of *Swietenia macrophylla* King, *Carapa guianensis* Aubl., and *Cedrela odorata* L. Proceedings of the Fourth SHIFT-Workshop, Hamburg, September 4-9, 2000.

8. Dünisch O., T. Schwarz, L. Gasparotto, V.R. Montóia (2000): Heartwood formation of plantation-grown and primary forest *Swietenia macrophylla* King, *Carapa guianensis* Aubl. and *Cedrela odorata* L. Proceedings of the Fourth SHIFT-Workshop, Hamburg, September 4-9, 2000.

9. Kriebitzsch W.U., O. Dünisch, H. Müllerstael, T. Schwarz (2000): $CO_2$ and $H_2O$ gas exchange of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. growing under controlled climate conditions in a greenhouse. Proceedings of the Fourth SHIFT-Workshop, Hamburg, September 4-9, 2000.

10. Noldt G., A.J. Kuhn, W.H. Schröder, J. Bauch (2000): Structure of fine roots of *Carapa guianensis* Aubl. and their uptake of mineral elements. Proceedings of the Fourth SHIFT-Workshop, Hamburg, September 4-9, 2000.

11. Noldt G. (2000): Charakterisierung der Feinwurzeln von *Swietenia macrophylla* King und *Carapa guianensis* Aubl. (*Meliaceae*) unter verschiedenen Standortbedingungen. Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg, Nr. 201, 127 p.

**Supplementary individual contributions**

(1) Thorsten Eilers (2000): Einfluß des Bodenwasserangebotes auf den Wasserhaushalt und die Wachstumsdynamik dreier Meliaceenarten unter Plantagenbedingungen in Zentralamazonien.

Diplomarbeit Fachbereich Biologie, Universität Hamburg, 141 p.
Attended by J. Bauch and O. Dünisch (ENV 42-2).

(2) Claudene Atayde (2000): Parametros anatomicos e tecnologicos de tres especies do genero *Hymenaea* L. em estado nativo e cultivado na Amazonia Central

Tesis de Mestrado, Universidade do Amazona/INPA, Manaus, 81 p.
Attended by M. de Freitas and O. Dünisch (ENV 42-2).

(3) Kikue Muroya (2000): Propagacao vegetativo da castanha do Brasil (Bertholletia excelsa H.B.R. e da sumauma (Ceiba pentandra (L.) Gaertn. pelo metodo de estaquia.

Tesis de Mestrado, Universidade do Amazona/INPA, Manaus, 71 p.
Attended by C. de Azevedo ENV 42-2).

(4) Alexandre Souza (2000): Propagacao vegetativo da castanha do Brasil (Bertholletia excelsa H.B.R. e da sumauma (Ceiba pentandra (L.) Gaertn. pelo metodo de estaquia.

Tesis de Mestrado, Universidade do Amazona/INPA, Manaus, 71 p.
Attended by C. de Azevedo ENV 42-2).

J. Bauch
(Univ.-Prof. Dr. J. Bauch)

O. Dünisch
(Dr. O. Dünisch)